OUTLINE OF GENETICS

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OUTLINE OF GENETICS

WITH SPECIAL REFERENCE TO PLANT MATERIAL

BY

MERLE C COULTER

Assistant Professor of Plant Genetics
the University of Chicago

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PREFACE

Probably no phase of science has ever developed more rapidly than has the subject of genetics during the last decade The number of competent investigators has so increased the scope of investigation has so broadened and the methods have so improved that there exists now an extensive literature on the subject The rapidity of its publication brings repeated changes in interpretation of the phenomena of heredity and keeps the subject in a state of flux For this reason it is difficult and perhaps even dangerous to prepare a textbook on genetics Some of the views expressed in the manuscript may be out of date when the book is issued It is evident therefore that the material of the present text can represent only one author s interpretation of the status of genetics in 1923

Plant Genetics by John M Coulter and Merle C Coulter was published in 1918 The present text is more than a new edition of the earlier one since it represents a thorough revision of the material presented The former title was felt to be an unfortunate one since it seemed to imply that the genetics of plants is something different from the genetics of animals Since the fundamental principles of inheritance are the same in the two groups of organisms and since it is necessary to use many of the results of animal investigation to illustrate certain points it is felt that a more appropriate title for the present text is *Outline of Genetics with Special Reference to Plant Material*

The primary object of the text is to meet a definite need felt by botanical students Such students in their contact with current botanical literature frequently encounter papers dealing with the genetics of plants and through lack of preparation are unable to grasp their significance Since this literature is far too important to be neglected it was thought advisable to provide such preparation in the simplest possible manner In addition to this need it is felt that the text will be useful to biological students for two important reasons In the first place the presentation is simple enough for students with little or no biological background to understand and in the second place the subject is brought more nearly up to date than in any earlier text This is especially important in view of the numerous significant investigations that have been made during the last year or two

In order to adapt the text to a greater variety of needs and interests an arrangement of material is made by means of which it may be used either as an elementary text or as one somewhat more advanced The material presented in large type provides a simple account which may be read coherently without reference to the material in smaller type The latter material presents a more intensive treatment of certain phases of the subject and will be of interest and value to those who wish to work out more thoroughly some of the details of investigation or application

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CHAPTER I

THE BACKGROUND OF GENETICS

Genetics or the experimental study of heredity was an outgrowth of the study of evolution A very brief survey of the subject of evolution before 1900 will serve therefore to provide a background for the material of the present text by depicting something of what was going on in the minds of biologists at the time that genetics had its birth It will also be useful to have before us some of the ideas of evolution as a means of suggesting a wider application of the principles of genetics that are to be taken up

Nothing need be said here of that phase of the evolution enterprise which concerned itself with convincing a doubting public of the mere fact of evolution The other phase involving the presentation of explanations of the evolutionary process will be sketched briefly

The vague ideas of evolution that occupied the minds of men during the earlier history of biology and the fantastic speculative explanations that were proposed have little more than historical interest for us today These explanations were based upon meditation rather than investigation so that they resembled philosophy rather than science

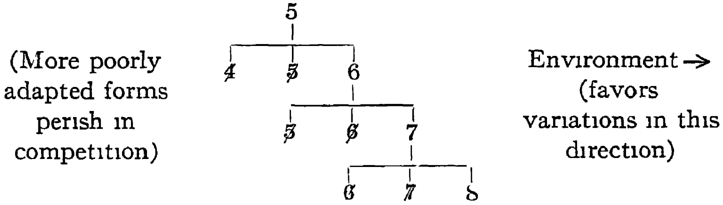
Around the latter part of the eighteenth century certain men (notably Erasmus Darwin Goethe and St Hilaire) developed more accurate notions of evolution based in good part upon their own observations and proposed simple explanations of the process These explanations called upon the direct influence of the environment but since little effort was made to analyze the process any further than this these theories have little value for us

The first author to provide any thoroughgoing explanation of evolution was LAMARCK and his theory of *Use and disuse* (1801) still commands the attention of biologists According to LAMARCK the environment was important not as a direct cause of evolution but merely as the occasion for evolutionary change When an animal came to live under changed environmental conditions possibly through migration it encountered certain new needs These new needs stimulated in the animal the desire to satisfy the needs Following this the animal made a conscious effort to satisfy the needs and in this effort succeeded in exercising certain of its organs more than before This exercise resulted in the development of the part exercised At this point LAMARCK introduces his basic assumption to the effect that acquired characters are inherited Whatever gain is made in developing an organ through exercise is passed on to the progeny The progeny living under the same environmental conditions and actuated by the same motives will make some further gain in the development of the organ in question and in this cumulative manner the organ will eventually be developed to such an extent that a new species may be said to have originated

The classic example which seems rather absurd in itself but serves to illustrate LAMARCK S ideas runs as follows The horselike ancestors of the giraffe come to live in a new and arid environment such that the only substantial forage is provided by the leaves of occasional trees These animals *need* to reach up to the leaves and therefore *desire* to do so Through a *conscious effort* to stretch up to the leaves their necks and limbs are *exercised* in such a way as to lengthen them The small gain in length possibly only an inch or less made during the lifetime of the individual is passed on to the progeny who are successful in adding another inch The final result is the giraffe This evolutionary scheme works also in the reverse direction as the result of degeneration through disuse

Absurd as some of Lamarck s illustrations may seem he has really provided the elements of a complete and not unlikely explanation of evolution The major objection lay in his assumption of the inheritance of acquired characters Practically all of the earlier experiments on this problem seemed to demonstrate that inheritance of acquired characters is impossible and it was for this reason that the majority of biologists discarded Lamarck s theory Another objection lay in the fact that conscious effort was hardly to be expected among plants Lamarck of course recognized this obvious difficulty and revised his theory in the case of plants where he claimed the changes were brought about through the *direct* effects of the environment citing such things as soil temperature moisture and mechanical pressure

The next great explanation was presented in Charles Darwin s *Origin of species* in 1859 Darwin called attention to the geometric ratio of increase among living organisms and reiterated the doctrine of Malthus to the effect that any population tends to increase more rapidly than the means of subsistence This increase tends to set up a severe struggle for existence or competition as the result of which an equilibrium of species is established with approximately the same number of individuals of a given species surviving year after year in any given locality Darwin next points out the universality of variation among living organisms such that no two individuals of any species are ever absolutely identical As for the cause of variation no explanation is provided but the nature of variation is rather clearly outlined Those variations which are important in the evolutionary process are characterized as quantitative continuous and fluctuating By quantitative it is meant that the variations are differences in the degree of development of some part or feature of the organism When it is said that the variations are continuous the implication is that further variations will take place in the same direction as the variations that have taken place in the preceding generations The term fluctuating indicates that reverse variations will take place as freely as do the progressive variations According to Darwin variation of this type is going on in all organisms Since this is true and since a severe struggle for existence is taking place it is impossible to escape the conclusion that it is the fittest that survive If a given species is represented in a certain locality by a thousand young individuals no two of which are absolutely alike and if there is only enough room or only enough subsistence for one hundred of them ever to reach maturity it must be true that in general it will be those that are the best adapted to cope with the conditions of the environment that are the ones to sur vive while the rest perish in the struggle The one hundred survivors are fitter than were the others of their generation because they happened to have certain useful organs or processes somewhat more fully developed In the following generation some of the progeny will have the organs in question still more fully developed than did their parents while on the other hand there will also be some that have them less fully developed The former group will again be chosen by nature to survive and perpetuate the species and thus progress will be made in the direction of better development of useful organs until a degree of development has been attained which may be said to represent a new species The way in which nature manipulates these quantitative continuous variations of DARWIN s to bring about this progressive evolution or adaptation can be visualized more concretely from this simple diagram


(More poorly adapted forms perish in competition)
5
~~4~~
~~5~~
6
~~5~~
~~6~~
7
~~6~~
~~7~~
8
Environment →
(favors variations in this direction)

The numerous objections to DARWIN s theory cannot be discussed here suffice it to say that these objections were directed mainly at the adequacy of the Darwinian variations in accounting for the results of evolution rather than at the idea of natural selection The survival of the fittest is a rather generally accepted idea The question whether the Darwinian variations are adequate can be considered more critically a little later in the light of the more recent knowledge of inheritance

The third great explanation of evolution was offered by De Vries in 1900 This author was the first to base his conclusions on the results of his own experimental breeding rather than merely on the extensive observation of plants and animals in nature Judging from the behavior shown by *Oenothera Lamarckiana* (American evening primrose) during the course of the ten or more generations that it grew in his garden De Vries concluded that the real basis of evolution lay in the phenomenon of *mutation* In addition to its normal progeny *O Lamarckiana* produced in small numbers certain distinctly new types the *mutants* The type of variation involved in mutation was distinctly different from the Darwinian being qualitative discontinuous and constant It was readily seen that the mutants involved qualitative changes from the parent inasmuch as entirely new characters were shown rather than merely the quantitatively greater or lesser development of certain of the parental characteristics It was equally plain that mutation was discontinuous the direction and nature of mutations being entirely unrelated to any of the mutations that had taken place in the past And finally the mutants were strikingly constant breeding true to their own characteristics rather than reverting in later generations to the original parental type These mutational changes that De Vries studied intensively in *Oenothera* were later identified in other species as well

The part that mutation may play in evolution is suggested by a consideration of the characteristics of the mutants Probably the majority of the mutants differ from the parent form in such ways that they might well be called degenerates the new characteristics shown serve to adapt the mutant more poorly to the environment than the parent was adapted Other mutants may show changes only of an unimportant type so that they are neither better nor more poorly adapted than was the parent A few of the mutants (according to De Vries) may show such characteristics as to be better adapted to the environment than was the parent form Upon this miscellaneous mass of mutants natural selection immediately comes to play quickly eliminating the poorly adapted types and preserving the good Thus De Vries holds with Darwin in invoking natural selection but the type of variations involved is distinctly different According to Darwin natural selection serves gradually to build up a new species according to De Vries numerous new species are born full fledged and natural selection merely decides which of them shall survive Objections to the De Vriesian theory will be mentioned later in this text in the light of some of the rather recent work in genetics

In addition to these three great explanations of evolution there are a few others that should be considered briefly A number of authors (notably David Starr Jordan in this country) have attached primary importance to the principle of isolation in evolution A few individuals of a species may migrate successfully to a new locality which is or may subsequently become sufficiently isolated by geographic barriers of one type or another from the original locality that no extensive return migration can take place The result is that a new colony is established which is sufficiently isolated from the parent realm that free crossing between the colonists and the stay at homes does not take place Any chance variations that may have existed in the few original emigrants will now have an opportunity to perpetuate themselves instead of being swamped out through free crossing with the other members of the parent species as would have happened if there had been no isolation Thus the various populations of a species that we see today somewhat isolated from one another have had a chance to express and later augment chance differences to such a degree that we may now regard them as different varieties With time the divergence of characteristics between the isolated groups will become still greater

The isolation theory as outlined above does not by itself provide a complete ’ explanation of evolution It is best to be regarded as a sort of a corollary to the Darwinian or De Vriesian schemes In either event it is the principle of natural selection that brings about progressive or adaptive evolution, while isolation either serves to multiply species on the same level through giving chance variations an opportunity to express themselves and become augmented, or else it serves to enlarge the scope of natural selection by thrusting representatives of the species into a somewhat new environment or by presenting natural selection with a slightly new population from which to make the choices

Another matter that should be mentioned is *orthogenesis* Orthogenesis may be regarded either as an explanation of evolution or merely as the name of a phenomenon There is considerable evidence supporting the belief that the variations (or at least many of them) that take place in living organisms are *determinate* taking place along predetermined lines in a predictable direction rather than *indeterminate* with an equal chance of their taking place in any direction, as the other theories would have it For example if a variant is slightly dwarfed as compared with the parent type there will be among the descendants of this variant a further variation involving greater dwarfedness and subsequently more changes will take place all involving further steps along this same predetermined line The direction of the variations is not necessarily related to any environmental demand

A few authors regarding orthogenesis as an explanation of evolution have visualized an intrinsic force in the organism which guides the variations Since this view has a vitalistic flavor it is not popular among scientific men More often it is simply recognized that a certain amount of variation of this sort does take place and orthogenesis is the name given to the phenomenon various quite materialistic explanations having been proposed to account for it

Evolution through hybridization is a theory that was suggested by Weismann some decades ago and has recently been developed and championed by Lotsy It is a fact well known among biologists that crossing two distinct types may result in the second hybrid generation in a few new and pure breeding forms somewhat different from anything that had previously existed Lotsy has shown by experiment that when such new forms (from *Antirrhinum* crosses) are returned to grow under natural conditions nature will select some of the types to survive but will quickly eliminate the others While there is little question that natural hybridization takes place and may be a real factor in producing new varieties at the same time this theory is not satisfactory as a complete explanation of evolution It seems rather obvious that although hybridization can multiply variations through crossing forms that are already different from each other it can never account for the original differences

In considering the relative merits of these different explanations there are three things that it is useful to bear in mind First it is certainly not necessary to subscribe to a belief in any one of the theories to the complete exclusion of the others It is quite possible that every one of them may be a factor in evolution and altogether probable that no one of them by itself can adequately account for all of the evolutionary change that has taken place

Second it is not advisable to contrast these explanations as though they were coordinate units The problem of evolution is not a single problem but a complex of numerous ones and any proposed explanation of evolution is confronted by the necessity of answering several distinct questions The conspicuous questions to be answered are

1 What is the cause of variation?

2 What is the nature of the variations that are important in evolution?

3 How may variations be perpetuated and multiplied?

4 How are the variations manipulated to effect progressive evolution?

It will be noticed that LAMARCK goes farther than any other author in answering question 1 Orthogenesis and the hybridization theory provide suggestions on this point but the suggestions are hardly satisfactory For question 2 rather distinct answers are provided by LAMARCK DARWIN DE VRIES and the orthogenesis theory It is in answering question 3 that the isolation theory and the hybridization theory have their chief value Question 4 is indirectly answered in one way by LAMARCK and indirectly answered in another way in the orthogenesis theory while all the other theories plainly call upon natural selection to answer this question If the theories are to be compared it can safely be done only after some such analysis as this

Third discussion of evolutionary theories usually leads to the realization that more exact experimental evidence is needed before much further progress can be made in solving the problems of evolution Such has been the actual history of the case for with the beginning of the twentieth century the study of evolution culminated in and became diverted into genetics the experimental study of inheritance Of course genetics has not answered all of the questions that have presented themselves in connection with evolution but many critical and suggestive findings have been made as will be seen in the following chapters and unquestionably genetics will contribute a great deal more in the next few decades

CHAPTER II

THE INHERITANCE OF ACQUIRED CHARACTERS

At the basis of genetics lies the fact that variation occurs in all living organisms It is possible to classify variations in a number of different ways At the outset it is important to realize the distinction between non-heritable and heritable variations As for the former it is usually evident that these originate as responses on the part of the organism to environmental stimuli Acquired characters of this sort however are of little significance in genetics inasmuch as they are not passed on from parent to offspring It is the heritable variations that provide the material of genetics and the origin of these is a matter of considerable controversy For the most part they are ascribed to mutation meaning that their origin is sudden and spontaneous seemingly unrelated to environmental stimuli There is some evidence however which suggests that heritable variations may originate as acquired characters It will be appropriate at this point to discuss the controversy on inheritance of acquired characters

The idea of inheritance of acquired characters was first clearly developed by LAMARCK in connection with his explanation of evolution the so called theory of appetency or the effect of use and disuse FRANCIS GALTON in 1875 was one of the first to express skepti

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A serviceable set of classifications is provided by BABCOCK and CLAUSSEN (1) cism in regard to such inheritance but it was WEISMANN (17) who was most influential in combating the idea After WEISMANN s presentation of the situation biologists were divided into two camps in reference to the question (1) neo Lamarckians who affirmed belief in inheritance of acquired characters and (2) neo Darwinians who denied it Until very recently at least the bulk of the evidence of genetics has served to refute inheritance of acquired characters

Much of the lack of agreement in this controversy is due to the definition of an acquired character It should be kept in mind that actual characters are not inherited but only the determiners which regulate the way in which the organism reacts to its environment For example when it is said that a child inherits its father s nose the statement is not meant to be literally true it is meant that just as there was something in the body of the father that was responsible for the development of a particular type of nose so there was a similar something in the child s body that developed a similar result It is merely a matter of convenience to speak of the inheritance of characters

WEISMANN defined an acquired character as any somatic modification that does not have its origin in the germ plasm This definition is not always easy to apply Examples of acquired characters in the WEISMANN sense are mutilations results of function (as in the use or disuse of certain organs) many diseases that affect the bodily mechanism and to use a rather vague expression effects of environment WEISMANN gave three reasons for rejecting the belief in inheritance of such characters (1) there is no known mechanism by which somatic characters may be transferred to the germ plasm (2) the evidence that such a transfer does occur is inconclusive and unsatisfactory and (3) the theory of the continuity of the germ plasm is sufficient to account for the facts of heredity

When Weismann says that there is no known mechanism by which somatic characters can be transferred to the germ plasm to him it is equivalent to saying that it is hard to see how the water that has gone over the dam can return and affect the flow of the water upstream He assumes of course that the germ plasm is isolated from the somatoplasm very early in the development of the fertilized egg into an individual and that when it is isolated it takes no active part in the history of the body (see fig 1) The somatoplasm is thus merely a carrier of the germ plasm and is unable to affect the character of it any more than a rubber hot water bag although capable of assuming a variety of shapes can affect the character of the water it contains (Walter 18)

This early differentiation of germ plasm and body plasm has been demonstrated rather strikingly in several animals In *Ascaris megacephala* the following cytological situation was demonstrated by Boveri in 1903 (Doncaster 7) Following the first division of the zygote the two daughter cells come to differ from each other through the apparent degeneration of some of the cell constituents in one That daughter which maintains the full cell equipment of the zygote thereby perpetuates the capacities of the germ plasm while the other daughter which has lost certain visible cell constituents

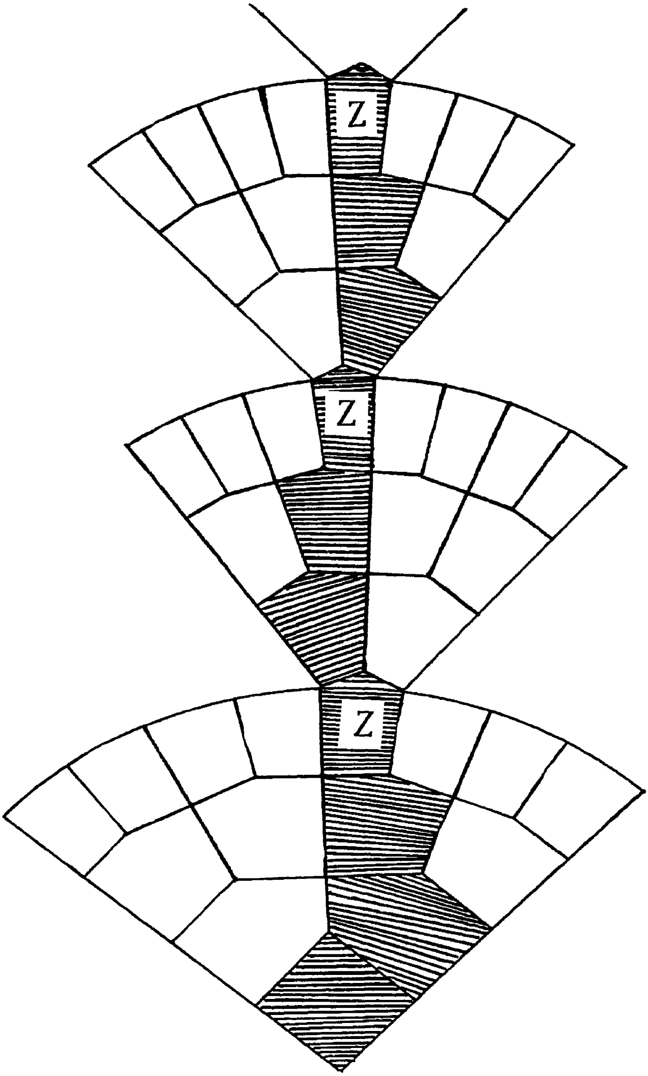

FIG. 1.—Diagram illustrating WEISMANN'S theory of germinal continuity. Three generations are represented with cells of germ plasm shaded and those of body plasm unshaded; germ plasm continuous from generation to generation, carried over from parent to offsping by zygote (*Z*); impossible for body plasm to perpetuate itself into a second generation.

starts a line of purely body plasm cells A similar differentiation occurs between the granddaughter cells from the fully equipped daughter and so on for two more divisions so that finally there are fifteen body plasm cells and but one germ plasm cell the germ cells of the adult individual can all be traced to this single initial

A somewhat similar program has been traced in Chrysomelid beetles where after numerous segmentation divisions some of the nuclei associate with certain granules and it is these nuclei that start the germ plasm HEGNER (DONCASTER 7) has succeeded in artificially destroying these granules by means of a hot needle thus producing embryos without germ cells

Equally striking situations have been demonstrated in other animals as well but nothing of the sort has ever been found in plants Germ cells in plants are formed from hypodermal and even epidermal cells which during earlier ontogeny are apparently identical with other somatic tissues Here there is surely no distinct germ plasm isolated from body plasm and insulated within it from environmental influences In fact there are cases in which adventitious” germ cells have been seen to form from tissues which normally are quite as somatic as any plant tissue could be In this connection it is worth mentioning that BATESON (2) suspects plants as genetic machines differ fundamentally from animals this idea being suggested to him in good part by the fact that in the animal the rudiments of gametes are often visibly separated at an early embryonic stage whereas in the plant they are given off from persistent growing points ’

A general theoretical objection to WEISMANN S view is that every organism is a physiological as well as a morphological unity and that cells completely insulated in such a unity would be impossible Cytologists also have come to believe that there are protoplasmic connections between adjacent cells in practically all plant tissues and in general physiology tends to confirm this Such suggestions voice a growing belief that the body plasm can affect the germ plasm

The reply of the Weismannians is that even though somatoplasm might affect germ plasm in this general physiological way this is a very different thing from the inheritance of some definite acquired character To be inherited such a character would have to be exactly redeveloped in the germ plasm and the influence referred to cannot be so specific as that This of course is a theoretical answer and the question can only be decided by experimental work A theoretical rejoinder to this answer may be suggested It is like the voice in a telephone transmitter which starts vibrations that make the receiver repeat the voice (Something more definite on this matter will be considered a little later) Before arriving at anything like a conclusion on this matter it will be necessary to consider some of the claimed cases of inheritance of acquired characters

1 MUTILATIONS —Most of the evidence under this head is in relation to animals It is a matter of common experience that mutilations are not inherited in man and the domesticated animals A few quotations from WALTER (18) suggest the situation

It is fortunate that the sons of warriors do not inherit their fathers honorable scars of battle, else we would now be a race of cripples The feet of Chinese women of certain classes have for centuries been mutilated into deformity by bandages without the mutilation in any way becoming an inherited character The progressive degeneration or crippling of the little toe in man has been explained as the inheritance of the cramping effect of shoes upon generations of shoe wearers but WIEDERSHEIM has pointed out that Egyptian mummies show the same crippling of the little toe and no ancient Egyptian could be accused of wearing shoes or of having shoe wearing ancestors

Sheep and horses with docked tails as well as dogs with cropped ears never produce young having the parental deformity WEISMANN S early experiments with mice later verified by other investigators give additional evidence that mutilations are not inherited He bred mice whose tails had been cut off short at birth and continued this performance through twenty two generations with absolutely no effect on tail length

Very little serious consideration has been given to the possibility of inheritance of mutilations in plants Cuttings for propagation are usually trimmed to prevent excessive transpiration but no one ever expects to find this mutilation perpetuated even in the plant developed from the cutting much less in the next generation developed from seed In fact since we have begun to learn of the remarkable powers of regeneration possessed by plants and animals we would not expect the inheritance of mutilations

There is one bit of work that should be mentioned in this connection BLARINGHEM (3) claims to have procured from a single injured individual a line of maize plants that show a varying per centage of double and sometimes triple grains The author calls this a typical case of inheritance of acquired characters but American investigators have hesitated to accept this interpretation of the phenomenon Characters of practically the same sort have been observed to originate in other cases in corn not known to have been injured in any way

2 EFFECTS OF USE AND DISUSE —Inheritance of the effects of use and disuse lay at the foundation of LAMARCK S theory of evolution WEISMANN was successful in discrediting this belief by explaining on some other basis practically all of the supposed examples of this phenomenon that had been advanced In plants of course it would be hard to find anything exactly analogous to the use and disuse of parts in animals LAMARCK himself did not attempt to apply quite the same theory to the plant kingdom

One fact however is a common experience of botanists Functionless organs gradually become aborted become mere vestiges or even suppressed entirely For example a study of the organogeny of flowers shows that when a floral member is belated in its development it is destined sooner or later not to appear at all The following theoretical Weismannian (or Darwinian) explanation of this situation is suggested A given species has a given nutritive capacity the less it draws upon its nutritive capital for the development of one organ the more it has available to expend on the development of other organs When an organ becomes functionless it no longer has any survival value survival is then dependent upon the relative development of the other organs Through variation certain individuals develop the functionless organ less than usual and therefore develop the other organs more than usual Under the new conditions these individuals will survive and the others will be eliminated Gradually abortion of functionless organs would take place in this way One would expect that the rate of change would be roughly pro portional to the size of the organ involved and that any retrogressive evolution of this sort would be slower than progressive evolution

3 DISEASES —Roughly speaking diseases are either the results of infection by bacteria or fungi or some inherent organic weakness Since the latter condition is chiefly serious only in inviting attacks by bacteria and fungi we are concerned chiefly with diseases caused by these pathogenic forms Realizing this true inheritance of disease seems to be an impossibility for if the parasite enters the germ cell it is practically sure to destroy it and there will be no progeny It is true that in many cases progeny are born diseased but this is due to reinfection of the young embryo from the body of the mother Many examples of this phenomenon are available in man and other mammals In plants also diseases (e g smut) are sometimes passed on by means of spores carried upon or even within the seeds Such a thing however can in no sense be spoken of as inheritance since it always involves a reinfection

In one respect however one may speak of disease inheritance Breeding experiments have shown that predisposition to disease and disease resistance commonly called susceptibility and immunity are inherited In practically all cases these characteristics are evidently of germinal origin having been hereditary in the beginning rather than acquired Such cases of course have no bearing on the present problem There remain a few instances however that rather suggest the inheritance of acquired characters

GUYER and SMITH (10) by inoculating female rabbits either with typhoid vaccine or with the living bacilli have succeeded not only in building up a high resistance to typhoid in these female rabbits themselves but in securing from them progeny with a high resistance In fact rabbits of the third generation have still shown a high immunity which could have come only from their grandmothers The likelihood however is that this immunity is not passed on through the germ cell itself but is reacquired ’ by offspring while in utero and nourished by the blood stream of the mother This of course would again be merely a case of ‘transmission rather than true inheritance The passing on of such an acquired immunity from the male parent to the progeny would constitute a convincing demonstration of inheritance of acquired characters but such a demonstration has not as yet been made

It is suspected that a situation similar to the foregoing exists also in man Racial immunity is believed by some medical men to have been built up not only through a natural selection of immune types but from the passing on from mother to offspring of acquired immunity

There is one fairly well known case of this sort in the plant kingdom BOLLEY (4) claims that he can get a resistant strain of flax from almost any known variety According to him the resisting ability increases from generation to generation if the crop is constantly subjected to disease attack He took a pure pedigreed strain of flax which had come originally from a single non resisting seed This was planted in slightly sick soil that is soil infected with the wilt producing organism Most of the individuals died but a few scrubs survived He then planted seeds from these in slightly sicker soil than before and thus by gradually work ing his crop into sicker and sicker soil in the later generations he finally obtained a fully resistant strain from the pure non resistant strain with which he started Such a strain he says will not lose its resistance if planted progressively in more infected soils He gives the following theoretical explanation of his results

Either (1) the so called unit character of resistance was present in undeveloped form and becomes stronger from year to year under conditions of disease or (2) there never was any character present which is entitled to be called a unit character but it began to develop the first year the parent plant came in contact with the disease and the protoplasmic nature of the ancestors of the plants which we now have has been such that they accumulated more and more the resisting power from year to year just as they had opportunity to develop resistance against a constantly acting factor of disease which when too powerful acts as an eliminating factor

Bolley inclines to the second alternative This general conception seems to explain why home grown seed is regularly more resistant than seed from the same variety which has had a vacation away from home for several years It has kept in training like a football player Bolley says that if these conclusions are correct there are probably no unit characters which are not fluctuating and there are no fluctuating characters which may not readily be fixed

These results are striking enough but their significance depends entirely upon the purity of the strains which were used originally and also upon the preservation of purity during the experiment Bolley s phrase elimination factor which he uses repeatedly, might be taken to suggest selection from an impure strain If his conception is true it could be demonstrated by developing a large majority of resistant individuals among the non resistant plants which were first subjected to disease attack rather than merely a few scrubs The results as they stand could probably be interpreted as due to the selection of a few resistant individuals from an impure strain

From the foregoing cases it becomes rather evident that so far as mutilations effects of use and disuse and diseases are concerned inheritance of acquired characters has not as yet been satisfactorily demonstrated either in the plant or animal kingdom One more category of cases however remains to be considered

4 EFFECTS OF ENVIRONMENT —This heading is sufficiently inclusive to include a number of types of cases

It has now been some years since CASTLE (6) performed his classic experiment on guinea pigs Animals with white coats will have only white coated progeny while a pair with black coats provided both male and female come from a pure stock will have only black coated progeny Using only animals from pure stock CASTLE removed the ovaries from a white coated female and transplanted them into the body of a black coated female The mating between this black coated foster mother and a white coated male resulted in a progeny all of which had white coats Evidently it was the germ cells alone that were effective in determining the character of the progeny The decisive results of this experiment were very influential in refuting the concept of inheritance of acquired characters At the same time it must be borne in mind that whereas such a superficial character as coat color might not respond to artificial manipulation of the germ cells it is still possible that there are other characters more fundamentally tied up with the metabolism of the organism that could be affected by such treatment

Numerous experiments confirmed these findings of CASTLE s but there was one field of investigation from which rather contradictory results began to be accumulated The numerous studies that have been made during the last few years on inheritance in the microorganisms have been ably summarized by JENNINGS (13) Here there appear some striking indications of inheritance of acquired characters

The germinal or genotypic constitution in most organisms is extremely stable in many stocks it changes not at all, so far as observation goes To alter it by physical or chemical agents is usually to kill it In some of the lowest organisms—rhizopods bacteria some infusoria—it changes with somewhat greater frequency though still rarely The nature of the changes and whether they may be permanent, or must after generations revert to the original condition is in some dispute In these same organisms environmental agents may produce changes persisting through many generations of uniparental reproduction and even through biparental reproduction the period of persistence depending partly on the number of generations through which the producing agent acted This suggests that inherited characters as permanent as any that exist might in time be so produced In spite of important differences of opinion among investigators to the reviewer the facts in uniparental reproduction seem to point more toward the production of evolutionary change by the action of the environment on the germ plasm than by any of the other methods

This behavior on the part of some of the lower organisms difficult to interpret without the assumption of inheritance of acquired characters fostered the following belief In higher animals where germ plasm and body plasm are sharply differentiated inheritance of acquired characters is an impossibility in the simpler organisms however germ and body plasm are doubtless one and the same thing with the result that a certain amount of inheritance of acquired characters can and does take place Such an opinion would not be out of harmony with the views of WEISMANN who was early forced to the belief that inheritance of acquired characters must take place in the more primitive organisms

The opinion of the biological world was becoming fairly well settled on this matter when GUYER S startling results (9) were published It will be seen that GUYER S methods strike at the germ plasm more directly than any that had previously been tried

Grinding up the eyes of white rabbits GUYER procured a lens extract This was injected into the blood stream of fowls There since the lens extract was a foreign and inharmonious protein a reaction took place which resulted in the production in the blood stream of an antibody (following the same principles which apply to the production of antitoxins in medicine) This particular antibody had the peculiar property of precipitating or in some way rendering functionless the characteristic protein of rabbit lens The property is quite specific so that this antibody may appropriately be spoken of as antilens Serum obtained from the blood of fowls thus sensitized and therefore containing antilens was injected into the blood stream of normal white rabbits No noticeable modification was obtained in any case upon adult rabbits that were so treated

When however the serum was injected into pregnant mother rabbits startling results were obtained Some of the resulting progeny had eyes that were clearly defective Furthermore the abnormality was readily transmitted through the female line for quite a number of generations without any additional injections being made The defect did not decrease in degree but seemed even more pronounced in the later generations

At this point a few questions might be asked Have such eye defects ever been known to occur among untreated white rabbits is this the sort of thing that might appear spontaneously through mutation or a recessive character that might have been segregated out through inbreeding as is true of so many other functional abnormalities? Careful inquiry has revealed the fact that no such eye defects have been reported elsewhere

Again is this the sort of thing that might be expected to result from any sort of mutilation or is it a specific response to a specific stimulus? This question is clearly answered by the behavior of the controls Untreated pregnant mothers mothers treated with serum from unsensitized fowls and mothers treated with serum from fowls that had been sensitized to rabbit tissues other than lens never gave any defective progeny

An even more critical question is the following is this another case of transmission rather than true inherit ance whatever may be the material basis of the defective eyes is it regularly passed from the body of the mother to the young in utero rather than through the germ cell proper ? The answer to this question was early suggested by the following facts Later litters from the mothers that had originally been treated never contained any defective individuals The influence of the antilens seems to die out in the blood stream suggesting that it is only by being incorporated in the germ plasm that the character can be perpetuated A more convincing demonstration of this point appeared in the later experiments Males with defective eyes when mated with females from a normal line produced only normal offspring When however these same males were remated with their own daughters from the foregoing cross a certain number of defective offspring resulted Evidently the abnormality can be passed on by a male parent it behaves in inheritance like a Mendelian recessive character Inasmuch as the male parent exerts upon the progeny no influence beyond what is contained in a single male gamete and inasmuch as this gamete is practically nothing more than a nucleus the foregoing amounts to about as clear a demonstration of inheritance of acquired characters as would be possible The very definite results of this set of experiments are sufficient to prove that inheritance of acquired characters can take place even in one of the higher animals where germ plasm and body plasm must be as sharply differentiated as anywhere It is equally true however that only very special conditions can produce the result

A word might be said on the theoretical mechanism involved Guyer proposes that there is some degree of constitutional identity probably protein homology between the mature substance of a tissue and its correlative in the germ and that basically inheritance is mainly a question of the perpetuation of specific protein complexes and development the result of differential reactions of these same fundamental constituents under different conditions of environment Is it unreasonable to suppose that if changes come to pass which affect certain constituents of tissue cells this influence if borne in the circulating fluids of the body could also affect the homologous constituents of the germ cells?

The same result has been obtained by the direct injection of lens extract into the blood stream of the rabbits themselves It is perhaps surprising that rabbits will manufacture antibodies for one of their own tissue It is evident that they do however and this brings us a distinct step closer to something that might occur under natural conditions If degenerating eyes may themselves originate antibodies which in turn affect the germ cells the cardinal principle of LAMARCK s theory of evolution through inheritance of acquired characters must be conceded

The fact that the eyes of the pregnant mothers were in no case themselves affected does not necessarily recommend the assumption of susceptibility only in the embryonic state but is doubtless due merely to the fact that there is a relatively much greater blood supply to the lens of embryo rabbits than those of adults

The experiments of GRIFFITH and DETLEFSEN final results of which have not yet been published promise to provide an equally good demonstration of inheritance of acquired characters in mammals (see Science 56 676–678 1922)

A few examples of the supposed inheritance of the effects of environment in plants should be considered ZEDEBAUR found that *Capsella* which in the course of many years had gradually crept along the roadside up into an alpine habitat and there acquired alpine characters retained these characters when transplanted to the lowlands This has been accepted by some as an authentic instance of inheritance of acquired characters but it is possible that this conquest of an alpine habitat by *Capsella* can better be explained by the gradual natural selection of just those germinal variations that best fitted individuals to cope with alpine conditions This would result in the gradual establishment of a strain of germ plasm that would produce body structures fitted to alpine conditions In other words this is just the way in which natural selection would develop a new elementary species from the original type If such a type were established of course its germ plasm would produce alpine plants even under lowland conditions They might not survive long and natural selection might eliminate them but their structure would be due not to the inheritance of somatic structures but to the inheritance of an alpine germ plasm

The objection to Zedebaur's conclusions on the grounds that the result may be attributed to natural selection has been avoided by the famous experiments of Bonnier (5) In 1884 this investigator began making plantations in the lowlands and at various altitudes in the Alps so arranged that the two individuals to be compared were produced by dividing one plant After a lapse of over thirty years he has made the following report A few of the plants taken from the plains to alpine stations died but a list is given of fifty eight species that proved able to maintain themselves at high altitude These have all undergone changes which make them closely resemble indigenous alpine plants In at least

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The principal changes are relatively large development of the subterranean as compared with aerial parts shortening of the leaves and of the internodes of stems increased hairiness and relatively larger development of bark and protective tissues The leaves become thicker in proportion to their surface and are a deeper green with more highly developed palisade tissue and a larger number of chloroplasts while the flowers are larger and more highly colored seventeen species the changes are so great that the plants have apparently been transformed into distinct alpine ‘ species The reverse experiment transplanting alpine plants to the lowlands gave similar but less startling results

These experiments as they stand are really more serviceable to the ecologist than the geneticist The geneticist wishes to know whether the transformations will maintain themselves when the plants are returned to their original stations and propagated by seed Bonnier has as yet made no clear statement on this latter point

An interesting issue arises in this connection If the transformed plants after being returned to their original stations revert in the course of a number of generations are we to conclude that inheritance of acquired characters has not taken place ? Should we not rather expect that if inheritance of acquired characters takes place under a given set of conditions the reverse conditions will bring the reverse change according to exactly the same principle ? Such work as that of Bonnier may eventually demonstrate that inheritance of acquired characters is a possibility in plants though it may fail to demonstrate that irreversible evolution can be brought about through inheritance of acquired characters The latter can be fully demonstrated only when an acquired character comes to be represented by a gene or set of genes in the germ plasm which are as definitely and permanently a part of the hereditary complex as any

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It is of course true that some evolutionary changes are probably irreversible (Herrick 12) but such changes are probably not involved in the Bonnier experiments of the pre existing genes Such a demonstration has as yet not been approached among higher plants it is approximated for animals by GUYER S white rabbit experiments

Attention should be called to another phenomenon which can easily be confused with inheritance of acquired characters If corn is planted in poor soil weak individuals result Seed from these weak individuals when planted in good soil will develop again somewhat weakened individuals suggesting the inheritance of acquired characters This however is merely the direct effect of environment continuing through the second generation The weak individuals in the poor soil develop small seeds with low nutritive capacity and plants developed from abnormally small seeds are always weak whether the individual that produced the seed grew in poor soil or not

There has been fairly good agreement on the point that trees deformed by prevailing winds like the willows that line the canals in Belgium and Holland or storm crippled trees along exposed seacoasts do not produce progeny showing these characters when the adverse environmental conditions are removed MAYR (15) has written a notable work on silviculture in which he claims that only species characters are inherited in trees and that the effects of climate are not inherited and therefore that the source of the seed makes no difference In other words seeds of Scotch pine would always produce Scotch pine progeny no matter at what latitude or altitude the ancestors had been growing According to MAYR therefore there is no inheritance of acquired characters in trees

Dr Arnold Engler (8) found however that in the seedlings in his nursery growth in height distinctly decreased as the altitude or latitude from which the seed came increased He also found that seeds from pines which had been crippled by growing in poor soil conditions gave rise to crippled plants when grown in good soil In many cases trees of the third generation still showed the habit acquired by their grandparents in different habitats

These are striking results but it is well to bear in mind all of the possibilities Engler might have been dealing with slightly different strains of trees differing in germinal constitution or it may have been another case of the false inheritance of acquired characters that was explained in connection with corn Seeds from higher latitudes and altitudes might well have been smaller so that we should have expected smaller progeny even when grown in the lowlands

There are several examples of what seems to be inheritance of acquired characters in simpler plants but opinion is not settled on interpretation of results Jennings statement (see p 24) includes the bacteria The work of Hansen (11) is interesting This investigator took isolated yeast cells which when cultivated under ordinary conditions uniformly gave rise to spore bearing forms and subjected them for a time to the highest temperature at which growth could still occur As a result he procured a race which has been cultivated under ordinary conditions for twelve years without once developing spores

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We have reason to believe the size of the seed may affect the size of the resulting plant even in such forms as coniferous trees (Munns 16)

As an example of the sort of thing that may occur among fungi the work of LONG (14) may be mentioned *Puccinia Ellisiana* and *P Andropogonis* both grow in one stage on *Andropogon* where they are to be distinguished by morphological differences in the uredospores *P Ellisiana* has *Viola* for its alternate host while *P Andropogonis* has *Pentestemon* *P Ellisiana* however has been artificially induced to infect *Pentestemon* where it produces spring spores that resemble those of *P Andropogonis* When these spring spores are returned to *Andropogon* the resulting uredospores are morphologically identical with *P Andropogonis* uredospores Conversely *P Andropogonis* can be made to infect *Viola* where it produces morphologically *P Ellisiana* spring spores and these will bring *P Ellisiana* uredospores when returned to *Andropogon*

This appears to be an actual change in species through a change in the quality of the nutrition But can it be demonstrated that the two forms were really distinct species in the first place?

The findings made by WILLIAMS (19) on periodicity of sex cells in the marine alga *Dictyota dichotoma* rather clearly indicate inheritance of acquired characters In any one locality the male and female organs originate simultaneously and pass through their successive stages of development together a general liberation of gametes and fertilization takes place on a particular day This period differs between different localities and varies slightly at any one locality at all times showing a clear relationship to the tides and therefore to the amount of light that reaches these submerged plants So intimate is the foregoing relationship that one can predict the time of liberation and fertilization by consulting the almanac of the locality On the other hand there is no evidence of periodicity in seas where there are no tides Plants transferred to aquaria in the laboratory and thus removed from the influence of tides and varying light continued to show the characteristic periodicity of the locality from which they came Thus an obvious adjustment on the part of the plant to a varying set of environmental conditions has evidently become heredity

It would be unwise to attempt any final conclusions on this subject of inheritance of acquired characters the status of the subject changes as new evidence is gathered Such evidence as we have considered however recommends the following tentative conclusion Inheritance of acquired characters is possible in many organisms This possibility is more often realized perhaps in the simpler than in the more complex organisms In the latter an unusual set of conditions is required such that the well insulated germ plasm will be reached

From the point of view of the geneticist the small amount of inheritance of acquired characters that might take place is usually negligible The geneticist deals almost entirely with characters the origin of which is either entirely unknown or spontaneous (mutation) and not clearly traceable to any specific environmental conditions For the evolutionist however this phenomenon becomes very significant The recent appearance of seemingly irrefutable instances of inheritance of acquired characters taken together with the growing conviction that mutation does not provide the type of change necessary to account for progressive evolution (see chapter on Mutation) is leading to a revival in modified form of the Lamarckian view

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CHAPTER III

MENDEL S LAW

Mendel s law is the basis of all work in genetics and should be understood from its original statement to its somewhat complex development In 1865 Gregor Mendel (3) published in the proceedings of a local scientific society the result of eight years of breeding experiments The publication was so obscure that scientific men in general did not see it and in addition to this Darwinism was at that time absorbing the attention of biologists For these two reasons Mendel s work remained unnoticed and of course unappreciated until it was discovered in 1900 and became the great classic of genetics Its influence therefore dates from 1900 rather than from the year of its publication

The substance of Mendel s experiments is as follows Wishing to discover the contributions of each parent to the make up of their progeny he chose for his work the simple garden pea which would breed rapidly and exhibited well marked varieties To magnify his results he secured hybrids by crossing distinctly different types of peas and to avoid confusion he considered only one character in each experiment For example he crossed peas which contrasted in character of height of flower color and of seeds In all cases he obtained similar results so that a single example will suffice Furthermore he discovered that it made no difference whether the staminate parent was a dwarf and the pistillate parent tall or vice versa and so for all the characters used In other words what are called *reciprocal crosses* gave the same results

The progeny of a tall parent and a dwarf parent were all tall This generation is known as the first hybrid or the F generation When this generation was inbred the progeny was made up of tall and dwarf individuals in a ratio of 3 1 This generation is known as the second hybrid generation or the F generation The dwarf forms of the F generation subsequently bred true producing only dwarfs Of the tall forms one third bred true and two thirds split up in just such a 3 1 ratio as did their immediate parents of the F generation This is expressed diagrammatically in fig 2

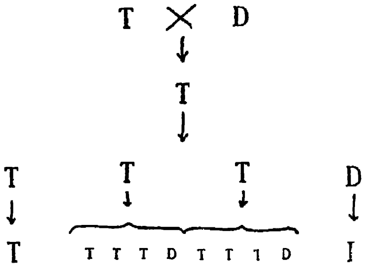

FIG 2 —Diagram illustrating visible results of MENDEL s experiments Cross between tall parent (*T*) and dwarf parent (*D*) gives hybrid progeny which are all tall hybrid progeny inbred gives 3 1 ratio in second hybrid generation inbreeding each of these four individuals separately gives for third hybrid generation results indicated in bottom line

MENDEL S theoretical explanation of this behavior involved three distinct theses

1 INDEPENDENT UNIT CHARACTERS —This means that an organism although representing a morphological and physiological unity from the standpoint of heredity is a complex of a large number of independent heritable units Thus if one pea plant is tall and another one is dwarf the behavior of the hybrid produced from them with reference to this character will be the same no

matter what other characters the parent plants may have had In other words the characters are independent units unaffected by other characters or units The character of tallness from a tall plant with wrinkled seeds or purple flowers will act just the same as from a tall plant with smooth seeds or white flowers Tallness is a unit and its behavior in inheritance is independent of all other units

2 DOMINANCE —In the germ plasm there are certain determiners of unit characters which *dominate* during the development of the body causing these characters to dominate over others and thus become visible The characters dominated over and thus not allowed to express themselves are called *recessive* characters These recessive characters may be present in the germ plasm but cannot express themselves and become visible as long as the dominant characters are present When a *dominant* character is absent however its *recessive* alternate is free to express itself and become visible

For example in the case of tall and dwarf peas tallness is a dominant character and dwarfness is its alternative recessive When a dwarf appears therefore there is present no dominant tallness to suppress it In the F generation all the individuals were tall because although they had all received the recessive character of dwarfness from one of the parents they had received the dominant character of tallness from the other parent and so dwarfness did not appear in any of them Such pairs of alternative characters are now commonly called *allelomorphs* Thus tallness and dwarfness are allelomorphs in the pea one dominant over the other which is therefore recessive

3 PURITY OF GAMETES —A gamete can contain only one of two alternative characters For example it may contain the character for tallness or for dwarfness but not both In other words allelomorphs cannot be represented in the same gamete If the gamete having the character for tallness unites with one having the character for dwarfness the resulting zygote will have both but will produce a tall individual because tallness is dominant to dwarfness When this tall hybrid produces gametes however one half of them will contain the character for tallness and one half of them the character for dwarfness Thus the alternative characters are segregated in gamete formation and no gamete will have both characters

These three theses independent unit characters dominance and purity of gametes (due to segregation) make up the theoretical explanation of Mendel s law Independent unit characters was of course a necessary conception It was original with MENDEL and has also been original with other investigators but this conception does not represent the essential feature of Mendel s law The idea of dominance had been somewhat vaguely proposed before MENDEL S time In the old literature on animal breeding one meets theories of prepotency which were proposed again and again before the discovery of MENDEL S work in 1900 In any event MENDEL was the first to formulate definitely the theory of dominance among unit characters It should be realized also that dominance is not an essential feature of MENDEL S theory Many cases are known in which dominance fails but in other regards the Mendelian inheritance is strictly followed

The essential feature of MENDEL S theory is his conception of the purity of gametes brought about by the segregation of alternative characters With MENDEL this was a purely theoretical scheme but since his time cytological investigation has discovered an actual physical mechanism which exactly satisfies the requirements of MENDEL S scheme Every living organism is composed of cells and these cells are endowed with nuclei Every nucleus contains a certain number of darkly staining bodies known as *chromosomes* The number of chromosomes is always the same for a given species At the cell divisions which take place in connection with the growth of the body each chromosome is very carefully divided in half so that the nucleus of each daughter cell has exactly the same equipment of chromosomes as the mother nucleus The exactness of this division in itself suggests that the chromosomes are the bearers of hereditary characters since none of the other cell constituents seems to be so accurately divided at cell division Even more significant is the behavior of the chromosomes in connection with gamete formation At that time it becomes evident that the chromosomes exist in pairs thus there is always an even number of chromosomes in every body cell of an organism The two components of each pair of chromosomes are always morphologically identical When the organism forms gametes a cell division takes place which is fundamentally different from the preceding cell divisions At this division no splitting of the individual chromosomes takes place instead the chromosomes line up in pairs and the nature of the division is such as to draw apart the components of each pair This is known as the reduction division for each of the resulting nuclei has the reduced number of chromosomes just half of the characteristic number in the body cells It is important to remember that this reduction is not indiscriminate but always involves a separation of the two components of each chromosome pair It is the reduction division that gives rise to the gametes Gametes therefore are characterized by the reduced or *haploid* number of chromosomes in contrast with the body cells which have the *diploid* number Gametes have just one representative of each chromosome pair that appears in the body cells When two gametes unite at fertilization there is of course a return to the diploid number in the resulting zygote

This is exactly the mechanism required by MENDEL S scheme on the assumption that the chromosomes are the bearers of hereditary characters So much data has accumulated to justify this assumption that it will be treated as an established fact in the subsequent descriptions

The chromosome mechanism may be applied to the case in hand as follows For convenience we will assume that the nuclei of the body cells in MENDEL S peas have each four chromosomes (two pairs) This is represented in fig 3 In the case of a tall plant two (one pair) of the four chromosomes carry the character for tallness that is something that determines the production of the tall character in the somatoplasm This unknown something is called by various names in the literature of genetics for the present we shall refer to it as a *determiner* In our illustration therefore two of the four chromosomes carry the determiner for tallness

Fig 3 shows a somatic cell with the diploid number of chromosomes In the formation of gametes this number is reduced to the haploid number which is in this case two The diagram shows that the reduction division separates (segregates) the two chromosomes carrying the determiner for tallness so that each gamete contains one This occurs for the other characters as well as for that of tallness From the tall plant therefore

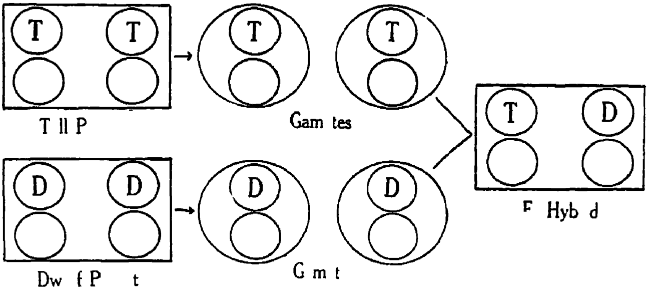

FIG 3 —Diagram illustrating behavior of chromosome in MENDEL S cross of tall and dwarf peas Large rectangular figures nuclei of zygotes or mature individuals large circles gametes small circles within zygotes and gametes chromosomes letters on chromosomes determiners (*T* tallness *D* dwarfness)

all the gametes will contain the determiner for tallness and from a dwarf plant all of the gametes will contain the determiner for dwarfness When these two individuals are crossed the zygote will contain both determiners and these two determiners will be transmitted together in the succeeding cell generations The individual developed from such a zygote will of course be tall but at the same time it will be carrying a recessive determiner for dwarfness and this fact will be shown by its behavior in breeding The result of inbreeding such hy brids is indicated in the accompanying diagram (fig 4) which represents the chance matings of the two kinds of gametes The obvious results are three tall individuals and one dwarf This is the so called *monohybrid ratio* which means the ratio when a single pair of allelomorphs is considered

Before discussing the further development of Mendel s law it will be necessary to explain some of the terminology of genetics When each gamete carries the same kind of determiner the resulting zygote is said to receive a *double dose* when a zygote receives only a single such determiner it is said to receive a *single dose* In fig 4 one zygote receives a double dose of tallness and two others a single dose These phrases are more or less common in the literature of the subject but the more frequent terminology is as follows When two similar gametes unite to form a zygote it is called a *homozygote* when the two pairing gametes are different the zygote is called a *heterozygote* Using this terminology it is evident that the 3 1 ratio of the F generation is really a 1 2 1 ratio as follows 1 homozygote for the dominant character 2 heterozygotes and 1 homozygote for the recessive character The 1 2 1 ratio therefore is the significant one and appears as a 3 1 ratio only because of dominance

In the experiment represented in fig 4 three tall individuals appear in the F generation Superficially the individuals look alike but it is realized that one differs from the other two in germinal constitution for one will produce only one kind of gamete while the other two will produce two other kinds To indicate this situation JOHANNSEN (2) has introduced some appropriate terminology Organisms which appear to be alike regardless of their germinal constitution are said to be *phenotypically* alike or to belong to the same *phenotype* On the other hand organisms having identical germinal constitution are said to be *genotypically* alike or to belong to the same *genotype* From the standpoint of phenotypes only MENDEL S F generation shows the 3 1 ratio but if genotypes are considered it shows the 1 2 1 ratio

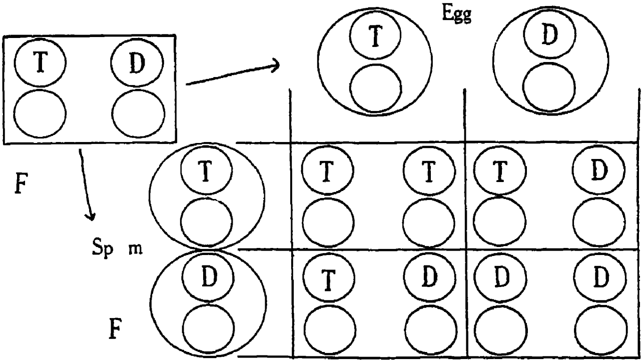

FIG 4 —Diagram illustrating behavior of first generation (F) when inbred Illustrates meaning of segregation and purity of gametes and how chance matings of I gametes result in ratio in F generation dwarf individual produced only by zygote in lower right hand corner

In other words this group of forms contains two phenotypes but three genotypes

Referring again to fig 4 several things may be inferred It can be seen what will happen in the F_3 generation when the F individuals are inbred The dominant homozygote will produce only dominant homozygotes in the F_3 generation the two heterozygotes will split up in the F_3 generation in the same 1 2 1 ratio as did their hybrid parents of the F generation and the recessive homozygote will produce only recessive homozygotes

It is interesting to consider what would happen if a heterozygote were crossed with a homozygous recessive It should be obvious that one half of the progeny would be pure recessives while the other half would be heterozygotes that is there would be a 1 1 ratio

Thus far we have considered only what is called the monohybrid ratio that is the ratio obtained from one pair of contrasting characters such as tallness and dwarfness The next step is to consider the *dihybrid ratio* MENDEL also used contrasting flower colors finding, for example that red flower is dominant to white flower Introducing this pair of contrasting characters into the situation we have been considering the dihybrid ratio will be the result Crossing a tall red flowered individual with a dwarf white flowered individual it is evident that all the F or first hybrid generation will be tall red flowered individuals since both of these characters are dominant In the F generation however the following ratio will appear 9 tall red 3 tall white 3 dwarf red and 1 dwarf white This 9 3 3 1 is the dihybrid ratio the explanation of which is indicated in fig 5 The question may be raised why the characters for tallness and redness are not represented on the same chromosome If they were the result would be a simple monohybrid ratio except that the tall individuals would always be red flowered and the dwarfs would always be white flowered The possibility of one chromosome carrying two different determiners will be considered later but at present we shall assume that these determiners are on different chromosomes

Fig 5 shows that we are dealing with two homozygotes each producing only one kind of gamete so that all the F progeny are similar both phenotypically and

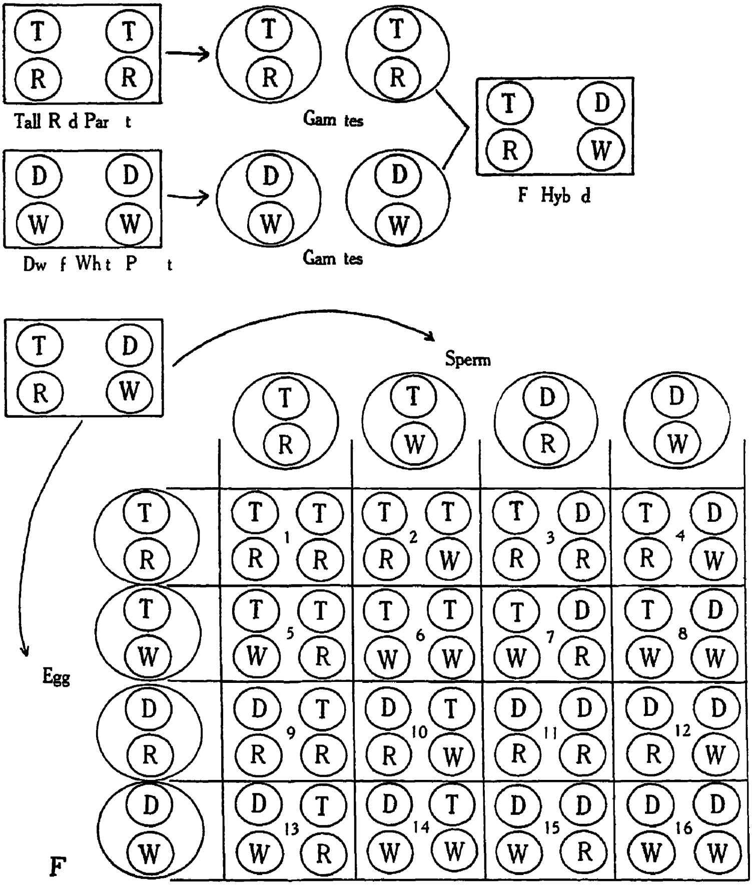

Fig 5 —Diagram illustrating dihybrid ratio Upper part shows how original parents were crossed to give F hybrid lower part shows F hybrid producing four kinds of gametes chance matings among these gametes when F is inbred results as indicated in the large set of squares and explains the 9 3 3 1 ratio in the F generation

genotypically, that is with the same appearance and the same germinal constitution Each of these F individuals will produce four kinds of gametes The possible combinations of these gametes that will occur when the F is inbred are expressed by the checkerboard The resulting F involves four phenotypes as follows nos 1 2 3 4 5 7 9 10 13 are tall red flowered individuals 6 8 14 are tall white 11 12 15 are dwarf red 16 is dwarf white This acounts for the 9 3 3 1 ratio

It will be noticed that nos 1 6 11 and 16 are homozygotes and therefore will breed true but the rest are heterozygotes either for one pair of characters or for both and these will split into various types upon further breeding

The higher polyhybrid ratios run into quite a string of terms but involve no further new principles For example the F phenotypic ratio for the trihybrid is 27 9 9 9 3 3 3 1 involving nine phenotypes (and 27 genotypes) but it can easily be worked out by the same method as was used for the dihybrid

Thus far we have been considering Mendel s law in simple form and have enlarged but little upon MENDEL S original statement The value of the law is apparent Upon its republication in 1900 it was taken up by biologists and numerous breeders set to work to test it As a consequence data for and against it began to accumulate As might be expected there was much apparent evidence against the law but as geneticists developed a better conception of the mechanism the contradictory evidence was explained away Almost every type of inheritance has now been explained according to Mendel s law A few of the more important cases will be presented

PRESENCE AND ABSENCE HYPOTHESIS

This may be regarded as a new method of Mendelian thought It was first suggested by CORRENS (1) but later was worked out in detail by other geneticists It is merely a different way of regarding the Mendelian mechanism For example in the case of a hybrid obtained by crossing tall and dwarf parents the result had been explained by MENDEL as due to the fact that one chromosome bears a determiner for tallness and the other one of the pair carries the determiner for dwarfness In other words each one of a pair of allelomorphs is represented by a determiner two determiners thus being present Dwarfness in this case would be the result of the interaction of that determiner and its environment during the development of the body and the same for tallness When both were present however the conception of the situation was as follows The determiner for dwarfness setting up its usual series of reactions early became paralyzed by the determiner for tallness or its products This result was called the dominance of the character for tallness It was as if the determiner for tallness completely prevented the activity of the determiner for dwarfness This conception was apparently borne out by the facts and was the explanation of the mechanism generally accepted

According to the presence and absence hypothesis however the situation is looked at from a different point of view Tallness is the result of a determiner but dwarfness is merely the result of the absence of the determiner for tallness The dominant character is produced by an inheritable determiner but the recessive character appears only when the dominant determiner is lacking This conception has some evident advantages and may modify the previous Mendelian diagram as shown in fig 6 This appears to be a simpler mechanism to account for the phenomenon called dominance In the case of the dwarf form there is a normal course of development in the case of the tall parent or hybrid however an additional determiner stimulates cell growth or cell division or both

This hypothesis introduces some additional terminology suggested by BATESON In our illustration the tall parent has two determiners for tallness and therefore BATESON calls it *duplex* having a double dose For the same reason the F individuals having only one determiner for tallness he calls *simplex* According to the same terminology the dwarf parent is *nulliplex* with respect to its character of tallness

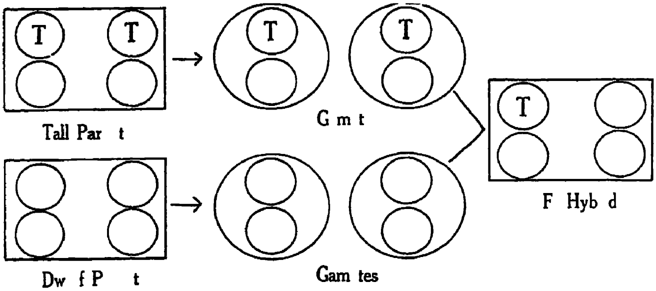

FIG 6 —Diagram showing how the original scheme must be modified to satisfy the presence and absence hypothesis

Additional advantages of the presence and absence hypothesis will appear later in connection with a consideration of *blending inheritance* and of *cumulative factors* in inheritance Attention however should be called to the fact that those who accept the presence and absence hypothesis do not use the form of notation thus far used in explaining Mendelian inheritance Assume that *T* is used to express the determiner for tallness the same letter (*t*) is used to express its absence For example instead of using *D* for dwarfness *t* is used for lack of tallness (fig 7) It is a matter of convenience to have a symbol to represent the recessive the absence of something that is present in another individual

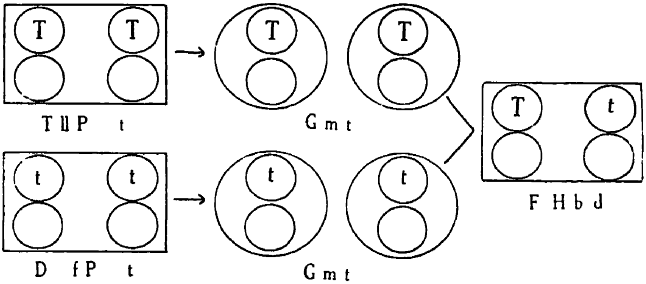

Fig 7—Diagram showing how presence and absence scheme is actually used with small letter representing absence

In summary the essential difference between the presence and absence hypothesis and that of dominant and recessive is that in the former case the recessive determiner has no existence at all while in the latter case it exists but is in a latent condition when associated with the dominant

As a matter of fact some of the later investigations have revealed cases that can hardly be accounted for by the presence and absence hypothesis In spite of these recognized exceptions however the scheme of notation employed under the presence and absence hypothesis has proved so convenient that it is almost universally employed

The checkerboard is an excellent method of depicting the mechanism at play but the same results can be obtained much more quickly and just as safely by another method Dihybrid (and other polyhybrid) ratios can be obtained by multiplying together the ratios of the monohybrid components (for this really amounts to the same thing as the checkerboard) In the present case one monohybrid component gives an F ratio of 3 tall 1 dwarf while the other monohybrid component gives 3 red 1 white (3 tall 1 dwarf) times (3 red 1 white) equals 9 tall red 3 dwarf red 3 tall white 1 dwarf white

The student will find it a very helpful exercise to work out for himself the various phenotypic ratios that will be produced by inbreeding the various genotypes shown in the F checkerboard and by crossing them in various ways In such problems the method of procedure is to work out separately the results for the different monohybrid components and then to synthesize these results The synthesis in this case amounts to simple multiplication

First of all one must familiarize himself with the various possible ratios encountered in connection with monohybrid crosses These are indicated in the following simple table (In every case the student must satisfy himself as to how the Mendelian mechanism brings about these results)

Crosses	PHENOTYPE	
	Red	White
RR × anything	1	0
Rr × *Rr*	3	1
Rr × *rr*	1	1
rr × *rr*	0	1

The solution of dihybrid problems then becomes a simple matter For example take the following cases

TtRr × *ttRR*

The monohybrid ratio as regards height is 1 tall 1 dwarf while the flower color ratio is 1 red 0 white Multiplying these together gives the dihybrid result 1 tall red 1 dwarf red

TtRr × *Ttrr*

The height ratio is 3 tall 1 dwarf while the color ratio is 1 red 1 white which results in the dihybrid ratio 3 tall red 1 dwarf red 3 tall white 1 dwarf white

BLENDS

This type of inheritance when first discovered was thought to be in direct conflict with Mendel s law It is a case in which dominance seems to fail for the two alternative characters both express themselves and the result is an average between them It is easy to explain this situation in accordance with the presence and absence hypothesis without any violation of Mendel s law

The classic example of blending inheritance was presented by CORRENS (1) in breeding work upon *Mirabilis Jalapa* the common four o clock CORRENS crossed red flowered and white flowered varieties and all the hybrid progeny had rose pink flowers This was a color blend distinctly intermediate between the colors of the two parents The F generation therefore seemed to contradict Mendel s law in that one color character was not completely dominant over the other The real situation however appeared in the F generation obtained by inbreeding individuals of the F generation which showed the blend By inbreeding the pink hybrids CORRENS obtained the perfect 1 2 1 ratio that is 1 red like one grandparent 2 pink like the hybrid parent and 1 white like the other grandparent Segregation was evidently taking place the only unusual thing being the appearance of the F individuals and that was explained immediately as failure of dominance (see fig 8)

The question this introduces therefore is that of a mechanism which would account for such a result The easiest explanation offered is that the red parent was a homozygote for redness (double dose) and the hybrid a heterozygote (single dose) the inference is that a single dose produces pink while a double dose produces red

A theoretical explanation of this occasional difference in the result of double and single doses is as follows Imagine that the body cells of a plant have a certain capacity for expressing hereditary characters In such a case just as a given quantity of solvent can dissolve only a given amount of solute so the body cells can express hereditary characters only to a definite limited extent In the four o clock a single dose of redness may be thought of as half saturating the body cells while a double dose completely saturates them In cases showing a complete dominance however a single dose completely saturates the cells and a double dose can do nothing more This analogy assists in visualizing on the one hand the necessary mechanism of blends (apparent failure of dominance) and on the other hand that for cases of complete dominance

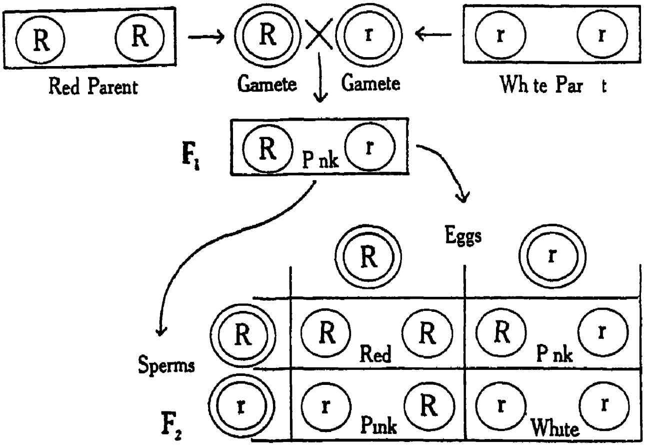

FIG 8—Diagram illustrating blending inheritance discovered by CORRENS in *Mirabilis Jalapa*

Problems dealing with determiners for which dominance is lacking differ from those where dominance is present only in so far as the monohybrid ratios must differ

Cross	PH NO C RA O				
	D m p t		D m l k g (H ph typ d g typ t th sam)		
	Red	White	Red	Pink	White
RR×*RR*	1	0	1	0	0
RR×*Rr*	1	0	1	1	0
RR ×*rr*	1	0	0	1	0
Rr ×*rr*	3	1	1	2	1
Rr ×*rr*	1	1	0	1	1
rr ×*rr*	0	1	0	0	1

For example take the following case where dominance is present for the height character and absent for the color character

TtRr×*ttRr*

The monohybrid ratio as regards height is 1 tall 1 dwarf while the color ratio is 1 red 2 pink 1 white Multiplying these together gives the dihybrid result 1 tall red 1 dwarf red 2 tall pink 2 dwarf pink 1 tall white 1 dwarf white

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CHAPTER IV

THE FACTOR HYPOTHESIS

Mendel concluded that each plant character depends upon a single determiner Inheritance however has proved to be a much more complex phenomenon than was indicated by Mendel s peas Ratios have appeared that were puzzling and geneticists have been forced to the conclusion that there may be a complex of determiners for a single character This conception is known as the factor hypothesis and much of the growing complexity of genetics has developed around this hypothesis Previously we have used the word determiner implying Mendel s idea that a single determiner is responsible for the development of a plant character and this has been true of the examples of inheritance previously considered It is understood now however that a character is frequently determined by the interaction of two or more separately heritable factors and hence the factor hypothesis The distinction between factors and determiners should be clear In case only one hereditary unit is involved in the production of a character this unit should be referred to as a *determiner* in case two or more units interact in the production of a character these are *factors*

This distinction of terms has pedagogical value but is frequently violated in the literature where factor is frequently used in the sense of determiner A less restricted term *gene* refers to the hereditary unit without implying whether it acts as a factor or simple determiner

1 COMPLEMENTARY FACTORS —This is the simplest expression of the factor hypothesis it may be illustrated by some of EAST s work (3) Crossing red grained and white grained corn this investigator obtained an F progeny which was all red This would suggest that the F generation would show 3 red to 1 white but instead it showed 9 reds to 7 whites which might seem to violate the Mendelian method of inheritance It is quite in accord with Mendel s law however if we consider that two complementary factors are necessary to produce the red character and that each of these factors is inherited separately Such a situation would give a dihybrid ratio as indicated in fig 9 It will be seen that out of the 16 individuals in the F checkerboard 9 will be red for they alone contain both complementary factors the other 7 will be white The situation is thus explained by the dihybrid ratio but although only one character is involved that character depends upon two complementary factors

Another situation is worth noting No 6 of the checkerboard is white because it contains only one of the necessary factors no 11 is white for the same reason but its germinal constitution is just the opposite What would happen if these two were crossed? There is only one possibility since each is a homozygote producing only one kind of gamete The result would be red and thus a cross between two whites would produce only reds What would be the result if nos 6 and 15 were crossed the former being a homozygote and the latter a heterozygote? It is obvious that the resulting progeny would be one half red and one half white The same result would be secured in crossing nos 11 and 14 A cross between nos 14 and 15 both of which are heterozygotes would produce 3 white to 1 red These

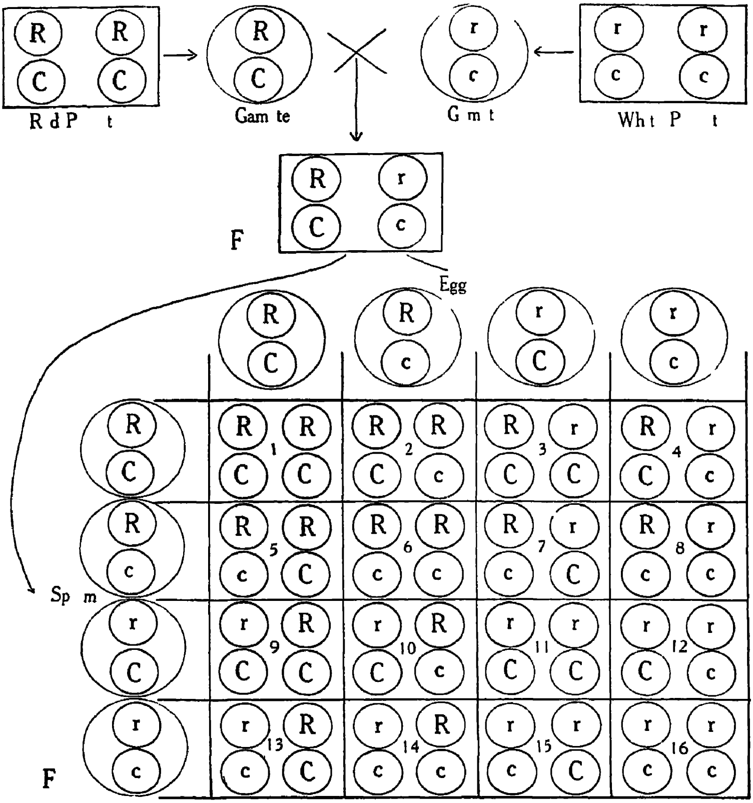

FIG 9—Diagram illustrating behavior of complementary factors in cross between red grained and white grained corn *R* and *C* must both be present to produce red grained corn

illustrations show how differently the same phenotype may behave in inheritance In each case 2 whites were crossed that is the same phenotypes but 3 different ratios were obtained because the genotypes were different

The striking feature of this situation is that one can cross two whites and get a red This gives an insight into the so called phenomenon of reversion For example in the course of numerous breeding experiments Bateson (1) obtained two strains of white sweet peas each of which when normally selfed bred true to the white color but when these two were artificially crossed all of the F progeny had purple flowers like the wild Sicilian ancestors of all cultivated varieties of the sweet pea This appeared to be a typical case of reversion Further breeding however showed that this was just such a case of complementary factors as we have been considering One of Bateson s white strains had one of the factors for purple flower color and the other strain had the other factor

It is interesting to note that if an investigator should cros homozygote no I with homozygote no II the F and F results would lead him to conclude that the red character was due to a simple Mendelian determiner *R* would remain a determiner until a strain of corn was discovered which lacked the *C* factor crosses with such a strain would reveal the real mechanism of the situation and thereafter *R* would be known as a factor

Complementary factors have been defined and the method of their inheritance described but is there any mechanism to explain the situation? A suggestion may be obtained from plant chemistry (2) The most prominent group of pigments in plants is the group of anthocyanins which are produced as follows Plants contain compounds called chromogens which are colorless themselves but which produce pigment when acted upon by certain oxidizing enzymes or oxidases This would provide a mechanism to account for the behavior of complementary factors If one of East s white strains of corn contained a chromogen capable of producing red but lacked the necessary oxidase it would remain colorless If the other white strain contained the oxidase but no chromogen it too would be colorless In crossing them however chromogen and oxidase would be brought together and a red grained hybrid would be the result In breeding such red grained individuals would of course give red and white progeny in a ratio of 9 7 as explained in connection with EAST s corn

It should be realized that the foregoing is no more than a suggestion So far as the genetics of the situation is concerned complementary factors may be regarded as an established fact but what either one of these factors actually amounts to in physiological terms has as yet only been guessed at In fact it would be safe to state that there is no known case where the exact physico chemical nature of any factor or determiner has been demonstrated In the foregoing instance neither chromogen nor oxidase may be the effective units involved There are however plenty of possibilities within the field of chemistry where the bringing together of two inert substances initiates a reaction sufficient to result in a new plant character Within limits hybridizing is very much like mixing chemicals in a test tube

The origin of complementary factors is an interesting field of speculation Did they originate together or separately? A natural inference would be that they originated together for neither would be of any use without the other It should be remembered however that the Darwinian idea of usefulness as explaining the occurrence of everything in a plant is frequently inadequate One must think rather of a plant as a complex physico chemical laboratory No one claims that all chemical reactions are useful they are simply inevitable and plant characters are the result of chemical reactions and physical necessities

The other alternative is to suppose that these factors originated independently in the plant s history In this case of course the first to be produced would remain functionless until its complement came into existence This might be an explanation of what have been called latent characters Also not only might they have originated at different times but in different varieties or species In this case if natural hybridizing should bring them together the result would be the appearance of a new character a few authors (notably LOTSY 5) believe that this is a very important factor in the origin of species

The behavior of the red grained and white grained corn serves as an introduction to the factor hypothesis and as an illustration of one of the important types of factor interactions Complementary factors are always to be recognized by the following behavior A complementary factor interacts with a dissimilar factor to produce a particular character

2 SUPPLEMENTARY FACTORS —A supplementary factor interacts with a determiner (or factor complex) to modify the character produced by the latter An excellent illustration of this factor type can also be provided by the inheritance of color in grains of corn (EAST 3) Interacting with the factors *R* and *C* is a third factor *P* This *P* factor is inherited quite independently of the other two but whenever it is present the red color becomes modified to purple The behavior of this factor is revealed when we consider the phenotypes to which the following homozygotes belong Corn of the formula *PPRRCC* has purple grains *ppRRCC* is red grained while *PPRRcc* and *PPrrCC* are both white grained From these facts one can draw the following conclusions (1) when *P* *R* and *C* are all present a purple grain results (2) red color can appear only when *P* is absent (3) *P* itself is entirely ineffective in the absence of either *R* or *C*

In the literature on inheritance in corn this factor is referred to by the symbol *Pr* its absence being denoted by *pr* (see work of EMERSON and others) It is to avoid possible confusion in the mind of the student that it is referred to by the single letter in the present text

These principles reveal the nature of supplementary factors Unlike complementary factors they never produce characters but merely modify characters already present Otherwise they follow the same principles of independent Mendelian inheritance with which we are now familiar

The student will find a very useful exercise in the solution of various problems which involve simultaneously several types of factors In solving such problems it is neither necessary nor advisable to employ any rule of thumb method As usual the checkerboard can be depended on to provide an accurate solution but this is too slow and cumbersome Instead the problems can always be solved rather easily by keeping in mind at all times the fundamental mechanism of inheritance that is at play and proceeding with the solution in a logical orderly manner (If the student simply remembers the Mendelian mechanism he can really work out his own methods of solving the problems)

In attacking polyhybrid problems the first principle to remember is to work out separately the solution for each pair of allelomorphs and then to put together these monohybrid solutions This putting together in the case of simple determiners amounts merely to multiplication as was described before but where factors are at play other methods of putting together are necessary In every case the method of putting together the monohybrid solutions is a rather obvious one and is clearly indicated by the definition of the factor type with which one is dealing

A few examples involving the *P* *R* and *C* factors will serve to illustrate In these cases one must consider the *P* factor last since it is effective only when both *R* and *C* are present

$$PPRrcc \times PpRRcc$$

Considering first the *C* factor one finds that a 0 1 ratio will result that is all of the progeny will lack the *C* factor Since this is the case one need go no farther with the solution since absence of *C* is sufficient in itself to insure that all of the progeny will be colorless or white

$$PpRrCc \times ppRrCC$$

Considering first the C factor one finds that a 1 0 ratio will result that is all of the progeny will have the C factor So far as C is concerned then all of the progeny may be colored

Taking up now the R factor it is evident that this will bring a 3 1 ratio that is ^{3} of the progeny have both C and R and will therefore be colored (whether red or purple will be decided later) have C but lack R and will therefore be colorless The final fate of this – is thus decided and one need give no further attention to this group The ^{3} however is eligible to be carried on for further consideration under the P factor

The ratio produced by the P factor is 1 1 that is – have P and $_{2}$ lack it So far as phenotypes are concerned however the present fractionation applies only to the $_{4}$ that was carried over making $_{8}$ with and $_{8}$ without P

Summarizing – have C but lack R and are therefore colorless $_{8}$ have C and R but lack P and are therefore red – have C R and P and are purple The resulting phenotypic ratio is therefore 3 purple 3 red 2 white

$PpRrCc$ selfed (equivalent to $PpRrCc \times PpRrCc$)

Considering the C factor the result is a 3 1 ratio or – with and without C The latter group $_{4}$ is hereby dropped since it must be colorless while the ^{3} is carried on for further consideration

The R factor also gives a 3 1 ratio or – with and without R But this fractionation applies only to the – that was carried on Therefore we have $\times$ or which has both C and R and $-\times$ or ^{3} which has C but lacks R This is hereby dropped since it also must be colorless while the is carried on for further consideration

The P factor gives 3 1 or $_{4}$ with and ^{1} without P This fractionation applies to the which was carried on so that we have $^{9} \times \frac{3}{4}$ or which has C R and P and is purple and $\times^{1}$ or ^{9} which has C and R but lacks P and is therefore red

Summarizing – plus ^{3} or $_{6}{}^{8}$ is colorless ^{9} is red and ^{1} is purple The phenotypic ratio then is 27 purple 9 red 28 white

(Any such mass of fractions is readily handled on the black board or scratch pad by considering the *C* *R* and *P* ratios under separate columns and scratching out fractions as they are disposed of by being carried on At the end if the procedure has been orderly the proper fractions will be found under the proper columns)

Other methods of solving these problems could be worked out All that is necessary in any method is clear vision of the Mendelian mechanism analysis into monohybrid components and separate solution of each followed by an orderly synthesis the method of synthesis always being indicated by the nature of the factors with which one deals

As before the physiological mechanism accounting for the behavior of the *P* factor has been only guessed at It has been found that the purple pigment is produced by the same substance as the red but represents a higher state of oxidation which suggests the following possibility *C* is oxidized by *R* up to a certain point where red is produced *P* an additional enzyme is capable of oxidizing the red pigment still further to purple *P* is incapable of attacking the original chromogen but when *R* carries the attack to a certain point *P* can function and carry the oxidization further As a consequence *P* without *R* gives white grains while *R* gives red grains only in the absence of *P*

3 INHIBITORY FACTORS —An inhibitory factor prevents the action of some other determiner or factor This factor type also can be illustrated in connection with inheritance of grain color in corn (EAST 3) If one were to cross a purple grained race of corn having the formula *PPRRCC* with any white grained race he would expect all of the *F* generation to be purple In this case every gamete produced by the purple parent would have the formula *PRC* As a consequence no matter what might be the formula of the white parent every F individual would have to have at least one dose of *P* *R* and *C* and this in itself should be sufficient to

insure the production of the purple color As a matter of fact just this result has been actually realized in practically all such crosses In one case however startlingly different results were obtained Crossing just such a purple parent as was mentioned with a white grained race resulted in an F generation which was all white

Inbreeding this F gave an F generation which contained some colored grains but a decided majority of whites Evidently the colorless condition is dominating over the colored This would be surprising in any case of color inheritance for we always expect colored to be due to the presence of something that is absent in colorless

Analysis of the present case revealed the fact that the white grained race that had been used was homozygous for the presence of an inhibitory factor *I* whenever this factor is present no color of any kind can be produced This readily explains the foregoing results If the purple grained race that was used had the formula *iiPPRRCC* and the white grained race was *IIPPRRCC* the resulting F would be *IiPPRRCC* which would be phenotypically white owing to the presence of the *I* factor Inbreeding would then result in the following F 1 *IIPPRRCC* phenotypically white 2 *IiPPRRCC* white 1 *iiPPRRCC* purple It is clear that the colorless condition is actually dominating but it is dominating on account of the presence of the *I* factor

It is evident that the purple and red types with which we had been dealing before must all have been homozygous for the absence of *I* Corn grains can be colorless for any of three reasons absence of *R* absence of *C* or presence of *I* whereas the colored condition occurs only when three conditions are simultaneously satisfied presence of *R* presence of *C* absence of *I*

Tetrahybrid problems involving *I* *P* *R* and *C* can be worked out on the same principles as were previously outlined It is probably most convenient to consider the *I* factor first

$IiPpRrCc \times iippRRCc$

Considering the *I* factor there will be $_2$ of the progeny with and $_2$ without *I* This first $_2$ is now dropped because it is bound to be colorless on account of the presence of *I* no matter what may be the rest of the germinal composition and in this case it is the latter $_2$ that is eligible to be carried on for further consideration

The *C* factor gives $_4$ with and – without *C* Applied to the $\frac{1}{2}$ that was carried on this becomes $_2\times_4$ or $_8$ without *I* and with *C* and $-\times$ or $_8$ without *I* and without *C* This last $_8$ is hereby dropped since it lacks *C* and must be colorless while the $_8$ is carried on for further consideration

The *R* factor gives a ratio of 1 with 0 without *R* Consequently no further fraction is dropped into the white phenotype at this point and the whole $\frac{3}{8}$ is carried on

The *P* factor gives $\frac{1}{2}$ with and $_2$ without *P* Applied to the $_8$ this becomes $_8\times_2$ or $^{3}_{6}$ which lacks *I* and has *C* *R* and *P* and is therefore purple and $_8\times_2$ which lacks *I* has *C* and *R* and lacks *P* and is therefore red

Summarizing $\frac{1}{2}$ plus $_8$ or [illegible] is colorless [illegible] is red and ^{3} is purple The phenotypic ratio is 3 purple 3 red 10 white

$IiPpRrCc$ selfed

I gives – with *I* $\frac{1}{4}$ without *I* Drop the $_4$ and carry on the

C gives $_4$ with *C* – without *C* Applied to the $_4$ that was carried on this becomes $\frac{1}{4}\times\frac{3}{4}$ or ^{3} which lacks *I* and has *C* and $_4\times-$ or ^{1} which lacks *I* and *C* both Drop the ^{1} and carry on the ^{3}

R gives ^{3} with *R* ^{1} without *R* Applied to the ^{3} that was carried on this becomes $-\times_4$ or ^{9} which lacks *I* and has both *C* and *R* and $-_6\times_4$ or ^{3} which lacks *I* has *C* and lacks *R* Drop the ^{3} and carry on the ^{9}

P gives ^{3} with *P* - without *P* Applied to the that was carried on this becomes $\times_{4}$ or which lacks *I* and has *C* *R* and *P* and is therefore purple and $\times_{4}$ or which lacks *I* has *C* and *R* and lacks *P* and is therefore red

Summarizing $_{4}$ plu — plus or is colorless is red and $^{7}_{6}$ is purple The phenotypic ratio is 27 purple 9 red 220 white

Thus three factor types are at play in the inheritance of color in grains of corn Four distinct factors are interacting but all are inherited independently and quite in accordance with Mendelian principles

Again the exact physiological nature of the *I* factor is not understood but can be only guessed at We have assumed that color is produced when an enzyme is present to oxidize a chromogen Enzymes are sensitive their activities may be affected or completely checked by various agents Assume that *I* is such an agent and the necessary mechanism is provided When *I* is present *R* is paralyzed so that it cannot oxidize *C*

4 CUMULATIVE FACTORS —These are considerably different from the other types and will be considered in another chapter under the caption Inheritance of quantitative characters

These four great factor types are really the only ones encountered in genetics each representing a distinct type of interaction In the literature of the subject many other descriptive titles are given to factors but no fundamentally new mechanisms are introduced

A few more words might be said on the three factor types that have already been considered Of these three the rarest type is the inhibitory factor complementary and supplementary factors being quite common

It is not surprising to find that true dominant inhibitory factors are rather rare as is suggested by the following reasoning In nature there has been for countless generations a struggle for existence among the individuals of a species with a survival of the fittest It follows from this that there has been a struggle for existence among unit characters Those dominant unit characters which are fit which serve better to adapt the organism to environmental conditions are the ones to survive while unfit dominant unit characters are eliminated with the elimination of the organisms that contain them (The same reasoning would not apply to the recessives which are protected from natural selection when they occur in heterozygotes) These dominant unit characters which exist today are for the most part survival characters being important in the economy of the organism since they are serving to adapt it to the environment In addition there must of course be a number of indifferent characters which cannot be construed as adaptations these have persisted simply because since they have neither positive nor negative survival value there has been no reason to eliminate them Since most of the dominant unit characters have positive survival value it follows that anything which prevents the expression of these dominant unit characters must have negative survival value This is exactly what the dominant inhibitory factor amounts to it is something which prevents the expression of a dominant unit character One is forced to the following conclusion Although dominant inhibitory factors may have come into existence just as frequently and numerously as the other types of factors and determiners most of these inhibitors would have been eliminated through natural selection on account of their negative survival value The few dominant inhibitory factors which persisted would be those which inhibited indifferent characters Color in grains of corn is doubtless an indifferent character

(There are two types of things which are fairly common and which might be confused with inhibitory factors (1) simple determiners which produce such characters as to mask other characters without really inhibiting other determiners (2) lethel factors which will be explained on p 69)

On the other hand it is not surprising to find that supplementary factors are rather common The supplementary factor carries further a reaction which has been brought up to a certain point by some other force Exactly this sort of mechanism must play a large part in the ontogeny of most organisms The litera ture of genetics is full of such things a intensifying factor diluting factors and distribution factors all of which follow the supplementary factor mechanism

Complementary factors are also common quite as we should expect Any complex machine contains numerous parts capable of applying numerous different forces each one of which may be quite functionless in itself but in interaction with some of the others will produce a visible result The living organism is just such a complex machine

It is not necessary that complementary factors exist only in pairs In corn itself there is an additional complementary factor *A* for color of grain (EMERSON 4) *R* *C* and *A* must all three be present for the grain to have color (A cross between the red type *AARRCC* and the white type *aarrcc* would give a red F *AaRrCc* and an F which would show a ratio of 27 reds 37 whites) Many sizable sets of complementary factors doubtless exist in the organism without our knowing it One can of course never identify a factor without discovering a race in which this factor is lacking Where the character involved is an indifferent one races lacking one of the complementary factors are frequently discoverable Where however the character involved is vital to the existence of the organism it is impossible to discover a race lacking one of the necessary complementary factors since such a race could not live In this connection a word should be said of lethal factors

Lethal factors of which a surprisingly large number have been identified during the last few years of investigation are by definition factors which bring death to the organism One might conclude from such a definition that these are inhibitory factors which are inhibiting some vital function of the organism but this is practically never the case In almost all cases it is the homozygous recessive condition only which brings the lethal effect so that it is really the absence of the factor that is lethal rather than the factor itself How are we to interpret this behavior in terms of the mechanisms which we have already described? One might assume that merely a simple determiner is involved a determiner for some vital function so that its absence brings the lethal effect On the other hand it is altogether likely that more than one gene is necessary to the success of this vital function On such a basis the lethal would be regarded as a factor rather than a determiner and would of course be thrown into the complementary factor class The present writer does not believe that genes should be called factors simply because there theoretically may exist other genes necessary to the production of the character in question but holds the view that the term determiner should be maintained so long as only one of the effective genes in the set has been identified In the case of the lethals however there have been discovered in the same organism (the fruit fly) a number of genes the absence of any one of which will bring the lethal effect It is reasonable therefore to regard these as composing one or more complementary sets governing the performance of certain vital functions

(The student may wonder how it is possible to identify lethal factors when their absence simply brings death an unrecordable phenotype in the population This will be understood later when the subject of linkage is discussed)

It should be realized that genes be they factors or determiners may at times have more than one role The *A* factor in corn mentioned above interacts with *R* and *C* in a complementary set for the production of aleurone color in the grain *A* also has an effect in producing pigment in the vegetative parts of the plant The *R* and *C* factors in stocks (SAUNDERS 6) are a complementary pair for the production of colored flowers *R* *C* and a third factor *H* must all be present for there to be hairs on the leaves Such phenomena support the belief that the gene is not a vitalistic unit endowed with a specific function in connection with a single plant character but rather is of the nature of many chemicals the presence of which will inevitably affect the course of more than one type of reaction

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CHAPTER V

INHERITANCE OF QUANTITATIVE CHARACTERS

This phase of the factor hypothesis if true is of fundamental importance not only to genetics but to general biology It is based upon the conception of cumulative factors and as it is presented it will be realized that it throws light not only upon numerous breeding problems but also upon variation in general which means evolution also A cumulative factor may be defined as one which when added to another similar factor affects the degree of development of a character

It will be recalled that Correns crossed red and white strains of *Mirabilis* and obtained pink hybrids The suggested explanation of this result was that a single dose of the red determiner gives pink while a double dose gives red When Correns inbred these pink hybrids he obtained the result presented in fig 8 that is 1 red 2 pink 1 white The mechanism in this case is quite evident

With this diagram in mind we shall consider some of the experiments of Nilsson Ehle (6, 7) at the Swedish Experiment Station He crossed two strains of wheat with red and white kernels The F individuals had light red kernels which of course suggests a repetition of the situation shown by *Mirabilis* in the experiment of Correns The F generation however showed a very different result The reds and whites appeared in the ratio of 15 1 but in addition to this among the 15 reds there could be distinguished varying degrees of redness Nilsson Ehle suspected that the 15 1 meant a dihybrid ratio 16 individuals being necessary to give the ratio so he constructed the tentative scheme shown in fig 10

This shows a regular dihybrid ratio except that the two factors involved are similar Applying the single dose and double dose conception as used in the case of Corren s pink *Mirabilis* we reach the following con clusions only no 1 has four doses and therefore it is deep red nos 2 3 5 and 9 have three doses and are somewhat lighter red nos 4 6 7 10 11 and 13 have two doses and are still lighter red nos 8 12 14 and 15 have one dose and are very light red while no 16 alone has no dose and is the only pure white This accounts for the 15 1 ratio and the different shades of red This is of course quite in accord with the Mendelian method of inheritance only two assumptions being necessary (1) that dominance is absent two doses having twice the effect of one (2) that the independent similar factors are cumulative in their operation This was Nilsson Ehle s conception and of course he tested it by further experimental work the results consistently confirming his assumptions

Since it is important to fix this conception clearly in mind another type of diagram may represent the facts even more clearly The proportion of the individuals showing the various degrees of redness in the F is graphically recorded in fig 11 each dot representing one dose of the factors in question

Continuing these investigations Nilsson Ehle next discovered a new strain of red grained wheat which when crossed with the pure white strain yielded 1 hybrids of an intermediate degree of redness as before

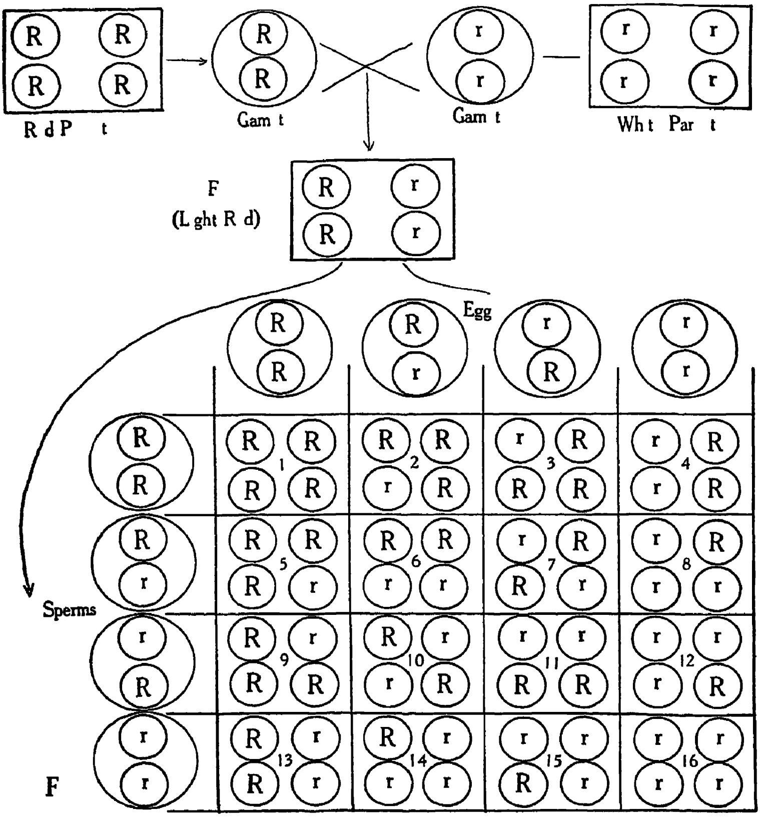

Fig 10—Diagram illustrating Nillson Ehle s explanation of 15 1 ratio obtained in F generation from cross between red grained and white grained wheat

The F generation however showed a different situation Reds and whites were obtained in the proportion of 63 1 the 63 reds as before falling naturally into differ ent groups on the basis of degree of redness Applying the same conception as before Nilsson Ehle discovered that in this case he was dealing with a trihybrid situation Without constructing the usual Mendelian checkerboard which would have to be extensive enough

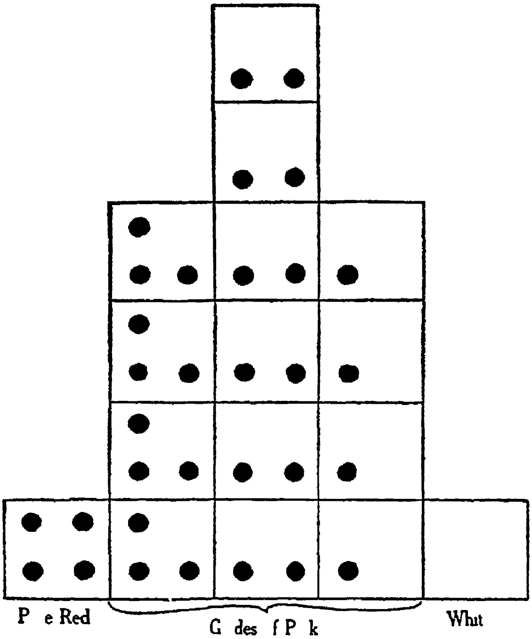

Fig 11—Another method of visualizing Nilsson Ehle's 1 1 ratio (see fig 10)

for 64 individuals the situation as it appeared in the F generation may be represented by fig 12 If this graph be surmounted by a curve we recognize the regular probabilities curve exactly the kind used by biometricians to represent fluctuating variations about a specific type

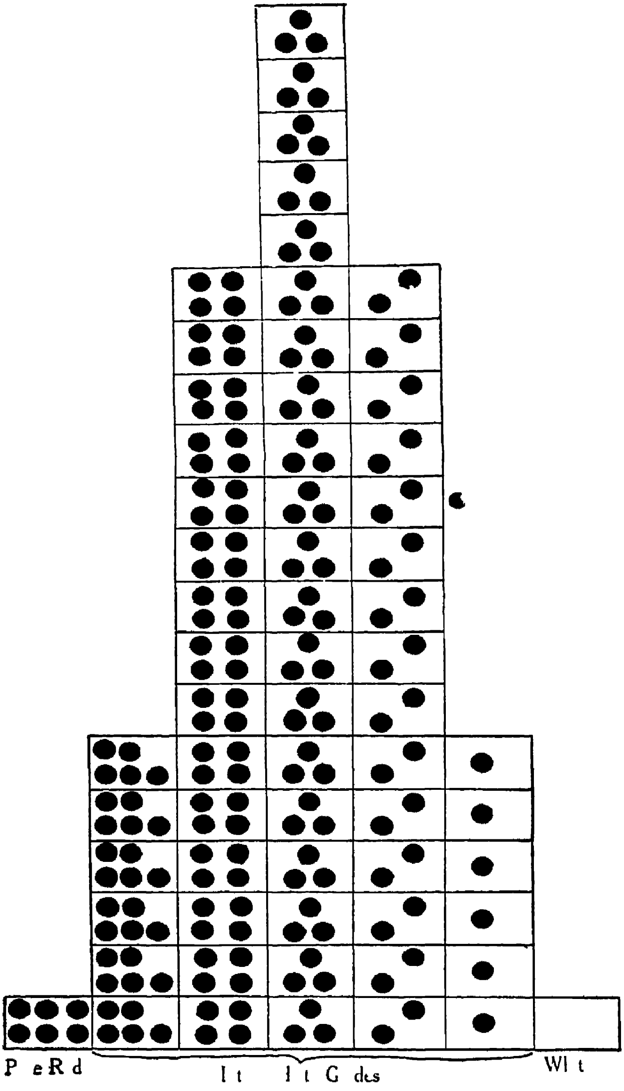

FIG. 12.—Diagram illustrating NILLSON EHLE'S 63 : 1 ratio

This conception of cumulative factors therefore has far reaching significance For a long time biologists have recognized individual quantitative variation within the species DARWIN depended upon it as the basis of his theory of evolution in fact ever since DARWIN S *Origin of species* individual variation has been fundamental in our conceptions To account for this universally recognized phenomenon DARWIN proposed his transportation hypothesis and WEISMANN offered his germinal selection both of which were unsatisfactory explanations Aside from these two attempts to explain individual variation no other comprehensive scheme had been presented Biologists had simply recognized the fact of individual variation without any clear conception of the mechanism

The importance of this new theory therefore is obvious It is an ingenious explanation of the inheritance of quantitative characters and of the existence of individual variations Furthermore the theory has not been developed through meditation but has its basis in scientific experiments It is imaginative to a certain extent as is every other valuable theory but unlike most such theories it has a substantial foundation namely Mendel s law

The importance of the possible role of cumulative factors in explaining individual variation which in turn may be the basis of a certain type of evolution has been emphasized because its importance has perhaps not yet been sufficiently appreciated It promises to be one of the most important theories of biology but of course will bear further testing by investigators

The doctrine of cumulative factors was further developed by Emerson and East (5) in their work with corn They were able to explain some of the ratios obtained by assuming three or four separately inherited cumulative factors just as Nilsson Ehle had done They obtained other ratios however which required more independent cumulative factors to explain Some idea of the extent of these investigations may be gained by noting the list of plant characters whose inheritance they explained on the basis of cumulative factors number of rows length of ear diameter of ear weight of seed breadth of seed height of plant number of stalks per plant earliness of flowering In all of these cases breeding gave the same characteristic results A cross between extreme parents gave hybrid progeny intermediate as to the character in question and in the F generation the two extremes reappeared along with all gradations of intermediate The relative frequencies of these classes always resembled the normal probabilities curve

Nilsson Ehle had been able to put his F intermediates into rather definite classes corresponding to the number of doses of the determiner each had received Emerson and East however could not do this with such exactness Their results showed all gradations but they could not distinguish any definite groups that is gradation was continuous and complete In other words they could not tell with certainty from outward appearance just how many doses of cumulative factors an individual contained Their results therefore do not seem so clear and striking as those of Nilsson Ehle but they are by no means vague and uncer tain For example even if they could not say definitely that a certain individual had three doses they could always say approximately how many doses it had and the breeding results always confirmed the idea of a number of cumulative factors at work For example a plant with three doses may vary with respect to the character in question It may approach the condition of the plant with four doses or it may vary toward the two dose condition Such variation may be explained by outside influences Any classification of the F individuals on the basis of the number of doses is more or less obscured by the influence of outside factors which are uncontrollable or at least uncontrollable as yet in breeding work

EMERSON and EAST have visualized these outside factors and discussed them In order to explain this discussion however we must recall a feature of genetics which has previously been mentioned Plant variations in the largest sense fall under two categories those due to (1) differences in gametic constitution and (2) those due to responses to environment The first category is the basis of all Mendelian conceptions while the second category includes such variations as are usually thought not to be inherited being acquired characters This category is now commonly called fluctuating variations

An illustration will make these two categories clear Assume that a plant with a determiner for tallness usually becomes 6 feet while one without this determiner becomes 3 feet The 6 foot plant however grown in good soil becomes 6 5 feet while in poor soil it is 5 5 feet In inheritance of course the 6 5 and 5 5 foot plants behave exactly alike the same is true of 6 foot plants It must be evident therefore that a classification of F individuals on the basis of the number of doses might well be slightly obscured If outside influences were lacking the F situation could be represented by fig 13

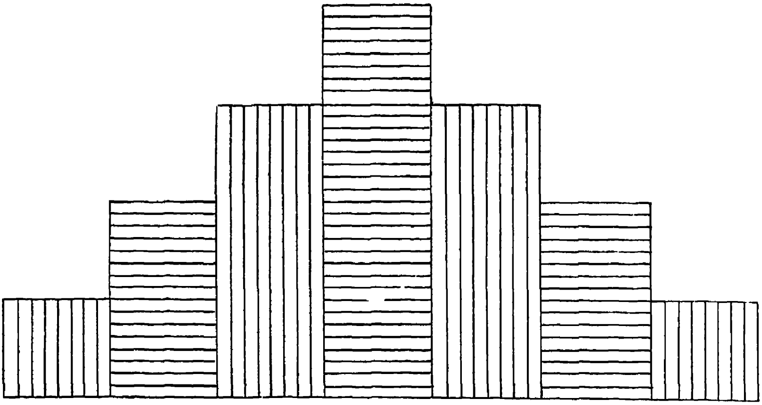

FIG 13 —Diagram illustrating distribution of phenotype classes in F population from cross involving cumulative factors Practically same diagram as fig 12 and interpreted in same way short rectangle at left indicates that very few plants of population contain maximum number of doses short rectangle at right indicates that very few plant contain minimum number of doses plants with intermediate number of doses most numerous as indicated by tall rectangle in middle (see also fig 14)

but when outside influences are active it may be represented by fig 14 It will be seen from this last diagram that not all individuals belonging to a particular size class may have the same number of doses that is conditions surrounding the development of a smaller dosed individual may be so much better than those for a larger dosed individual that they may exchange size classes in the result In this way the results of germinal constitu tion may be somewhat obscured by the varying external conditions of growth

Another factor that may obscure these results is what is called physical correlation For example a corn plant of small size but with the hereditary capacity for producing large ears could not fully express this capacity It could not produce as large ears as it it had been a large sized plant

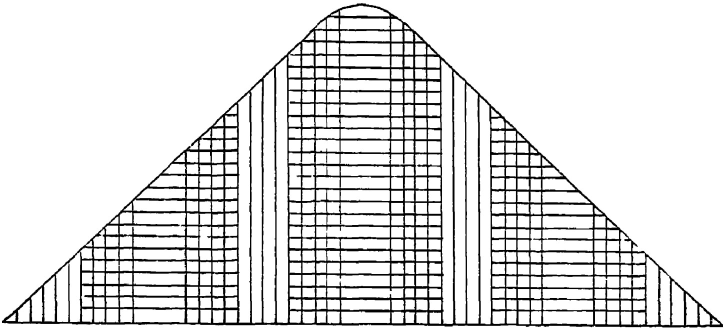

FIG 14—Diagram illustrating how environmental influences may obscure phenotype classes of F Overlapping of phenotype classes makes possible that two apparently identical plants might actually have a different number of doses diagram also shows that while breeder could not recognize whether a plant had two or three dose he could distinguish between plants of two and four doses etc Thus intelligent selection could be effective

Such are some of the conditions or factors that tend to obscure results in the F generation and give rise to ratios hard to interpret The weaker the influence of these factors the more clearly do the phenomena of cumulative factors come out The total result of this phase of the work of EMERSON and EAST in spite of obscuring conditions that have arisen, has been to strengthen greatly the conception of cumulative factors A summary of their conclusions is stated as follows

‘ When one is dealing with quantitative characters that is those produced by cumulative factors he is confronted by exactly the same principles of Mendelian inheritance as have long been known to apply to qualitative characters With quantitative characters however the problem is more complex due chiefly to two things (1) we are usually dealing with more factors and factors cumulative in their operation ( ) the significance of the breeding results is usually somewhat obscured by the natural fluctuations due to response to uncontrollable factors in the environment

In connection with the cumulative factor concept a modifying statement should be made as to the mechanism involved Heretofore it has been assumed that we are dealing with numerous separately inherited factors absolutely identical in their nature cumulative in their effect No doubt one might regard with suspicion such a seemingly artificial mechanism Probably it would be easier to believe if it were modified in the following manner Instead of assuming that the numerous factors are identical in function we may assume that each of these factors has its own peculiar function but that that function plays a part directly or indirectly in developing the quantitative character in question For example suppose height is the character One of the factors determines the development of numerous nodes another increases the amount of chlorophyll another determines the size and vigor of the root system another brings early germination and a long growing season Such factors although not identical will be cumulative in increasing the height of the plant Of course a single dose of one type of factor may not bring the same increase in height as would a single dose of one of the other types and therefore the mathematics of the situation will be slightly modified The fundamental mathematical system however will remain the same and we will have the satisfaction of dealing with a natural mechanism rather than an artificial one

A few of the applications of the cumulative factor hypothesis are worth considering Assume that a practical breeder crosses two extreme parent types in the hope of obtaining a hybrid combining the desirable characters of the two parents If the material is corn he might use one parent with large grains but few in number while the other parent had many grains but small ones Such quantitative characters as these would be determined by cumulative factors and the hybrid would be intermediate with respect to both of these characters that is the grains would be of medium size and medium number No matter how many crosses he made he would always get this result and not the desired combination of large grains and many of them

Suppose now that these intermediate hybrids are inbred in the hope of obtaining the desired combination among the individuals of the F generation It will be realized that the chances of obtaining a plant combining the two extreme characters of large grain and numerous grains would depend upon the number of factors that enter into the make up of these quantitative character Assume that there are five factor pairs in each case The mathematics of the situation would show that in order to get the desired pure type from a cross between two parents each having their desirable character determined by five pairs of cumulative factors it would require 100 acres of corn to have an even chance of getting one such individual in the F generation It is altogether unlikely that any farmer would use 100 acres and a corresponding amount of labor on such an extreme chance Even an agricultural experiment station would not feel justified in conducting such an experiment

The question arises whether there is any way of avoiding this impossible situation The escape is suggested by the fact that time can take the place of numbers EAST has shown that by growing 1000 individuals in the F generation 100 in the F and 50 in the F_4 one stands as much chance of getting the desired combination as by growing 250 000 in the F provided an intelligent selection is made in each generation In other words one who understands the mechanism of the inheritance of quantitative characters will grow only 1000 individuals in the F generation and will select for seed only those individuals with the most favorable combination of factors In this way by intelligent selection factors are piled up in the right direction from year to year In a few years the desired result will be reached without the necessity of ever growing a very large number of individuals Such work is practicable at experiment stations and it is the kind of work that a number of them have been doing Even the farmer is able to accomplish this Although his selection of individuals is not quite as intelligent as that of a scientific breeder he is at least selecting in the right direction and making some advance A little more time and a little more acreage would bring him very close to the desired goal

A further application of the cumulative factor hypothesis may be considered The practice we have been discussing under the title of inheritance of quantitative characters seems to be little more than what has already been called artificial selection which is the oldest of all methods of plant breeding It is a method that was thought to be discredited entirely by the work of DE VRIES and JOHANNSEN when they discovered elementary species or pure lines and demonstrated that artificial selection could never result in any large or permanent improvement In consequence of this artificial selection as the most important method of securing desirable races gave place to pedigree culture at a number of experiment stations The older method was not entirely abandoned for it had its uses but many regarded it as a medieval method of breeding The artificial selection which we have been describing however is distinctly different from the method practiced by the early breeders In brief statement the difference is as follows

The selection proposed is preceded by an intelligent hybridizing and after that genotypes rather than phenotypes are selected that is the selection is made on the basis of germ plasm rather than body plasm This would be a sufficient reason for the superiority of the new method of artificial selection as compared with the old A little further analysis will make the difference clearer

In the old method of artificial selection the breeder in the first place is dealing with such germinal variations as happen to appear in his crop and in the second place he is dealing with those fluctuations which appear as responses to the environment When he selects a large plant to use for seed that plant may be large on account of its germinal constitution but on the other hand it may be large because it is growing in a less crowded place or a place more heavily fertilized than the others In that case the large plant might not furnish good seed The plant breeder of the old method undoubtedly made such unfortunate selections frequently that is he selected on the basis of external appearance and external appearance is very often a poor index of hereditary capacity Furthermore he would not keep his lines pure but would deal constantly with an unmanageable mixture of good and mediocre types Intelligent selection is based on germinal constitution only—by keeping careful pedigree record a selection of genotypes is possible—and therefore its results are quicker and surer It is really a pedigree culture rather than a mass culture method

Another phase of the subject should be considered When a plant breeder is trying to improve his crops by selection for quantitative characters although he uses the old method of selection he is likely to be making some gain as the experience of hundreds of years has shown The germinal constitution of his crop plants is masked by fluctuations of course but this mask is not complete Most of the plants he selects are bound to possess high numbers of factors of the right kind and he probably rejects most of the plants with few factors In any event he has generally succeeded in the long run in getting a somewhat improved race

A summarized statement of this situation may be helpful Our recently developed knowledge of the inheritance of quanti tative characters seems to justify artificial selection but it does not justify the old blind method of selection It emphasizes the need of intelligent selection and shows how such selection can be made In order to do this one must understand the mechanism of inheritance involved and must make his selection on the basis of genotype rather than phenotype All along the line strains must be discarded which though recommended by the phenotype of one of their ancestors are to be condemned on the basis of their breeding capacity Selection is always to be made on the basis of breeding capacity that is genotype

The situations just considered enable one to understand two phenomena which have been baffling scientific plant breeders for some years The races of plants improved by artificial selection have usually reverted to type when selection ceases This fact was recognized for a long time but was first pointed out clearly by De Vries (3) Since then we have always expected this result that no improvement will maintain itself but will run back unless the selection is continuous When a practical breeder announces that he has developed by selection a new race which continues to breed true without further selection we are inclined to disbelieve him for we know that only elementary species breed true We explain that the practical breeder bases his selection on fluctuations and therefore his new race is bound to revert to type It is obvious now that there is a flaw in this argument The practical breeder may be basing his selection on fluctuations but at the same time he may be piling up cumulative factors in the right direction Thus he *might* eventually secure a race containing all the cumulative factors Such a race would be a homozygote and could not help breeding true Most of the claims of artificially improved races that breed true may be false but it should be remembered that such a thing is possible and may be stumbled upon accidentally even with unscientific breeding

There is another phenomenon which has been much discussed and which can now be explained in the same way This is the so called fixation of hybrids For years breeders have made promiscuous crosses and then begun artificial selection with the F generation Eventually they have secured a pure breeding new type It will be remembered that it was in this way that

EAST worked with the quantitative characters in corn and the explanation is the same

In addition to the practical value of the conception of cumulative factors the theoretical value is worth considering for it explains things that have been very vaguely understood This conception suggests that the origin of species by natural selection in the way described by DARWIN a method which for some time has been thought impossible may actually be possible within limits

Of course natural selection in a certain sense has always been accepted almost as generally as the fact of evolution The point in dispute is as follows DARWIN used as the basis of natural selection those small individual variations which we have come to call fluctuations the same kind of variations the old plant breeder used in his artificial selection DARWIN claimed that such variations could be piled up until the result would be a new species It was in 1900 that DE VRIES showed in convincing way that this kind of variation never resulted in a new species at best it only developed a race which approached the boundary of the species and never crossed it Moreover such a race would revert to type rapidly as soon as some slight change in conditions set up a new standard for selection This argument confirmed by experiment has been generally accepted

We now know that individual variations are not always mere fluctuations or responses but may be due to varying doses of cumulative factors A selection on this basis may very well result in a new race that breeds true and a race that breed true is DE VRIES definition of a new species To reestablish DARWIN S ideas on the origin of species is certainly an important consideration The situation illustrates how genetics and evolution are tied up together so that neither one of them can be appreciated fully without some knowledge of the other

A few words may be said in reference to the reversion of an old race to its original specific type DE VRIES outlined the situation clearly and his conclusions are generally accepted It is doubtful however whether it has ever been understood since no one has ever devised a reasonable mechanism for such a reversion The conception of cumulative factors supplies this mechanism A new race developed by natural or artificial selection among individual differences means the piling up of cumulative factors in a given direction Stop the selection and the old plants with the small numbers of factors are allowed to survive reproduce cross with the others and eventually bring back the species to the original average condition

One very seldom has any occasion to work out problems on cumulative factors since here the phenotypes do not show up as clearly as they do in connection with the other factor types Any such problems however could readily be solved by some such method as the following Remember that we are dealing with a dominance absent situation and represent the number of doses as exponents attached to the numbers which indicate the frequencies of the different classes

AaBbCc×*AABbcc*

The *A* set gives a ratio of 1 with two doses 1 with one dose and should be represented as 1 1

The *B* set gives 1 with two doses 2 with one dose 1 with no dose and should be represented as 1 2 1 (1 1)×(1 2 1) equals 1^4 3^3 3 1

The *C* set gives 1 with one dose 1 with no doses or 1 1 (1^4 3^3 3 1)×(1 1) equals 1^5 4^4 6^3 4 1 The final result is 1 with five doses 4 with four 6 with three 4 with two 1 with one

During the last decade the mechanism of cumulative factors has been invoked to explain a great many of the phenomena of genetics One noted instance of this will be worth considering as it has a very important bearing upon one of the fundamental concepts in connection with the mechanism of inheritance

A few years ago geneticists might have been grouped into two schools mutationists who believed in the introduction of new hereditary units by mutation alone maintaining that the hereditary genes were invariable and could not be modified by selection and selectionists who believed that the genes could be modified by selection The most prominent figure among the selectionists was Castle and the main experimental evidence upon which he based his view was as follows

Castle (1) isolated a race of rats which had a black and white coat pattern known as hooded (the black pigmented area hav ing the location and general shape of a hood) This hooded pattern bred approximately true and behaved as a simple Mendelian recessive in crosses with rats of the wild type These facts naturally led CASTLE to believe that hooded was a simple Mendelian unit character represented in the germ plasm by a single gene

CASTLE then commenced selection For twelve generations selections were made from this new race without a single outcross that is every generation was inbred (brother and sister matings) thus insuring the constant purity of the stock In one series selection was made for an increase in the extent of the pigmented areas in another series selection was made for decrease in the extent of these areas The result was that the areas in the one series steadily increased while in the other they steadily decreased CASTLE pointed out that (1) with each selection the amount of regression (running back) grew less that is the effects of selection became more permanent in other words in each succeeding generation there was a decreasing tendency to revert to the original average type (2) advance in the upper limit of variation was attended by a like advance of the lower limit The total range of variation therefore was not materially changed but there was a progressive change in the point about which the variation occurred In other words it was like the progressive shifting of the center of a circle the diameter of the circle did not change but the position of the circle determined of course by its center was gradually changing These were the two important facts which CASTLE brought out and they have been stated approximately in CASTLE s own words

Fig 15 will help make the situation clear The average amount of variation in any one generation of the pure stock (the diameter of the circle referred to) is indicated by $\xleftrightarrow{A}$ Of course even pure stock varies somewhat since no two individuals are exactly alike biology recognizing what is called individuality The point is that the comparatively small variation in a pure stock is not due to germinal differences but to responses called out by varying external conditions such as nutrition light etc These response variations usually called fluctuations vary with different individuals but the hereditary capacity of all of them remains the same A selection on the basis of fluctuations within a pure line therefore should not result in any permanent improvement in fact it has been demonstrated many times that no such improvement can be effected in this way When selection is made

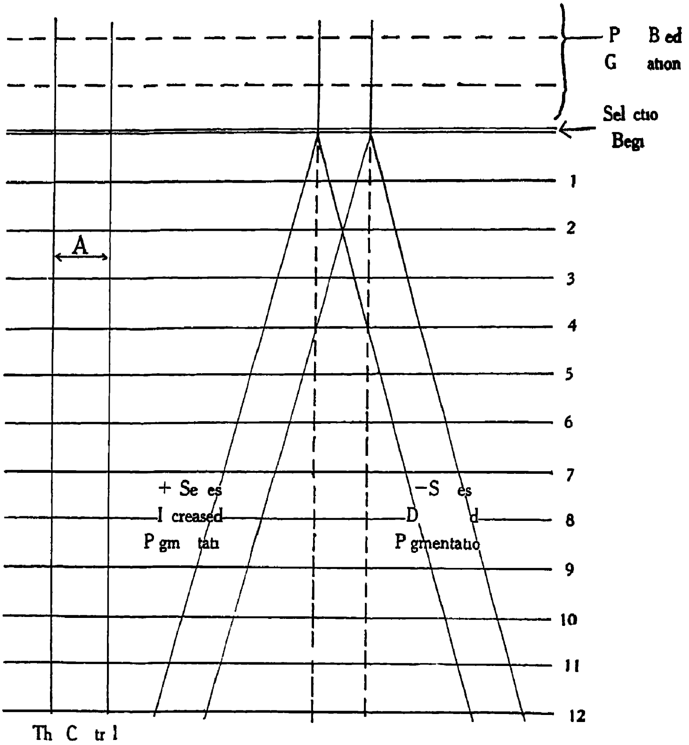

FIG 15—Diagram illustrating CASTLE'S selection experiment with hooded rats

however among varying doses of cumulative factors an entirely different situation is faced for in such a case we are not dealing with a pure line

The significance therefore of CASTLE'S results may be realized He bred his original pure line for many generations and found that it varied only within very narrow limits and these slight variations he regarded as mere fluctuations Furthermore he found that the character of his pure line behaved in crossing as a simple unit character and that no complex factors were involved With this evidence he should not have been able to effect any permanent changes by selection but this is exactly what he did Selecting in opposite directions he developed two new strains the boundaries of the new strains being distinct from one another and distinct from the boundaries of the original strain that is the non selected type that he started with

CASTLE s next step was significant He crossed each of his new strains with the same wild race the result being that each of his new strains behaved as a simple and distinct recessive unit The high pigmentation strain came out of the cross with the characteristic high pigmentation the low pigmentation strain came out with the characteristic low pigmentation

The conclusion from this series of experiments may be given in CASTLE s words as follows The conclusion seems to me unavoidable that in this case selection has modified steadily and permanently a character unmistakably behaving as a simple Mendelian unit The importance of this conclusion is evident Mendelism had been based upon the conception that unit characters could not be modified Mendelians of the mutationist school had granted only two possible methods for the origin of new races (1) by recombinations of existing characters through hybridizing (2) by the sudden and complete dropping out of an existing unit or the equally sudden addition of a new unit both of which possibilities might arise from mutation No mutationist would grant however the possibility of modifying an existing unit character the thing which CASTLE claimed to have done basing his claim upon well controlled experimental breeding If CASTLE s contention were true it would result in the fundamental modification of Mendel s law The whole mechanism would have to be modified to take into account new fields of variation that had not been thought to exist

The statements of the mutationists in reference to these experiments should be considered They attempted to explain CASTLE s results through the cumulative factor mechanism The claim was made that CASTLE had started with a character that had fluctuated continually never having been brought to as small a variability as have most other characters The question was raised whether CASTLE's assumption that this variability was merely due to fluctuation was altogether justified Might not the variability have been due to varying doses of cumulative factors? Suppose for the moment that this were the case it would not be surprising that CASTLE could develop two diverse strains by selection for selection would result in piling up the cumulative factors in one direction or the other CASTLE's rejoinder was that if this were a cumulative factor situation why had none of the extremes appeared in the non selected stock which instead bred approximately true? The answer was made that the extremes did not appear in the pure bred stock merely because of the mathematical limitations If one is dealing with six cumulative factors and the so called pure stock has an intermediate number of doses there could not be much chance of getting out the extremes in a single generation It would be necessary to secure over 4000 progeny to have an even chance of getting one such extreme or about 50 progeny to get anything that would very noticeably approach the extreme It would seem therefore that CASTLE's chances to determine this would be very small Rats certainly do not produce 4000 progeny in a single generation in fact they produce much les than 50 therefore CASTLE's pure stock went on in the intermediate condition and only by selection could he pile up the factors and reach either extreme

Thus far the explanation seemed satisfactory CASTLE showed however that the coat pattern condition behaved in crosses as a simple Mendelian unit that is it did not split up into complex ratios but came out as a recessive in a regular 3 1 ratio This really involved no difficulty Suppose CASTLE crosses one of his pure strain rats having the hooded character with another race that has some pattern character that conceals the hooded character If this other character is a simple Mendelian one the result of the cross would be the ordinary monohybrid ratio that is in the F generation from such a cross the ratio of hooded to non hooded (with the hood concealing character) would be 1 3 which in fact is exactly what CASTLE got At the same time the amount of pigmentation determined by numerous cumulative factors might go on in the same intermediate condition unaffected by the cross The relation of pattern to non pattern is merely a simple monohybrid system temporarily superimposed upon the other more complex system without permanently affecting it any more than any inhibitory factor permanently affects the factor it inhibits or a dominant permanently affects a recessive

It was in this way that the mutationists attempted to explain away Castle s results Castle did not at first admit the adequacy of this explanation but continued to maintain that he had modified a unit character by selection and some geneticists agreed with him

This question might be raised Why cling so strongly to the cumulative factor hypothesis and force Castle s results into this conception ? Is there anything sacred about a unit character that it should not be modified just as complex chemical molecules may be modified in certain reactions ? Why not admit that Mendelian factors may be modified and explain Castle s results in this way The reason is that when we begin to admit that unit characters and single Mendelian factors may be modified the whole conception of inheritance becomes chaos The great advantage of the factor hypothesis is that it furnishes the clearest method of describing breeding results East (4) makes an eloquent statement on this point

> Taking into consideration all the facts no one can well deny that they are well described by terminology which require hypothetical segregating units as represented by the term factor What then is the object of having the unit vary at will ? There is then no value to the unit the unit itself being only an assumption It is the expressed character that is seen to vary and if one can describe these facts by the use of hypothetical units theoretically fixed but influenced by the environment and by other units simplicity of description is gained If however one create a hypothetical unit by which to describe phenomena and this unit varies he really has no basis for description

The question was finally settled in a very neat way by some critical breeding experiments that Castle himself performed on these same hooded rats (2) The degree of pigmentation on the high pigmentation strain was designated as +3 73 (in terms of certain arbitrary units) while the low pigmentation strain was −2 63 Critical examination revealed the fact that the cross between the +3 73 strain and the wild race brought a slight reduction in the amount of pigmentation as it appeared in the extracted hooded recessives in the F Repeated recrossing of these extracted individuals with the wild race finally resulted in extracted hooded rats of the grade +3 04 No further reduction was possible in this way These results could be explained by the following assumptions The hooded pattern is modified in degree of pigmentation by a varying number of doses of cumulative factors (as the mutationists had previously maintained) The wild race is characterized by having a certain number of doses of these cumulative factors The repeated crossings and extractions mentioned above would eventually result in producing rats which had the hooded pattern plus that number of doses of cumulative factors which was characteristic of the germ plasm of the wild race Since it was found that repeated crosses with the wild race could bring the degree of pigmentation down to +3 04 and no lower it was felt that +3 04 was the degree of pigmentation which would be produced by that number of cumulative factors which was characteristic of the wild race

The critical test of these assumptions could be made through a similar manipulation of the low pigmentation strain If the assumptions were correct the low pigmentation strain should be raised finally to +3 04 by repeated crossing with the wild race CASTLE performed this experiment and got exactly this result one of the families from the low pigmentation strain (−2 63) being finally brought up to +3 05

These results naturally caused CASTLE to change his views on the matter and served rather generally to establish the views of the mutationists The situation depended for its interpretation upon the cumulative factor mechanism (Here it was felt that the cumulative factors were not primarily responsible for the production of the character in question but served merely to modify the degree in which it expressed itself Other cases of the same sort have been encountered elsewhere the mechanism at play being commonly referred to in the literature as multiple modifying factors)

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CHAPTER VI

LINKAGE

The fundamental mechanism of inheritance which was proposed by MENDEL and which was later supported by cytological studies has been confirmed time and again by breeding experiments Its scope is considerably enlarged by the factor hypothesis but its basic concepts are not altered It will now be necessary to consider some well established facts of inheritance which can be interpreted only by analyzing still further the hereditary mechanism

It has been assumed that the chromosomes are the bearers of the hereditary units or genes (The term gene is used where it is not intended to imply whether the hereditary unit acts as a factor or determiner) This has been warranted by the fact that the distribution of the chromosomes in inheritance fits exactly into the Mendelian scheme In the cases that have been considered in the last few chapters the genes have always been located on separate chromosomes with the result that they have been passed on in inheritance quite independently of each other The intensive study of inheritance that has been made during the last decade however has revealed cases where the total number of genes known for the organism exceeds the number of chromosome pairs The obvious conclusion is that more than one gene may be carried on a single chromosome If this is true it should result in decided modifications of the breeding results Conversely the occurrence of a certain type of breeding result would serve as a clear indication that more than one gene may be carried on a single chromosome and thus as a further confirmation of the belief that the chromosomes are the bearers of hereditary characters

In 1911 results of just this sort were obtained in corn by EMERSON (2) who stated This is an example of a feature which is probably very widespread in the plant world but of which at present we know little Long before any further important work was done along this line among plants however MORGAN (5) published the results of his very careful and intensive breeding experiments with the fruit fly His ideas have had a profound influence upon subsequent work in genetics He has given us a more accurate picture of the hereditary mechanism and one that fits the facts better than any previously proposed In simplest terms the picture is this Each chromosome is a rodlike structure and numerous genes are arranged in a line along this rod Thus MORGAN further analyzes the germ plasm by accurately locating the genes (He does not attempt any description in physico chemical terms of the genes themselves or of the exact relation they may hold to the chromosomes on which they are carried)

We cannot discuss here the many ways in which this fundamental conception has cast light upon work in genetics Suffice it to say that it has resulted in a new school of geneticists whose experiments have been more intensive more exact and in some ways more fundamental than those of any previous school To date most of the linkage work has been done with the fruit fly but a great deal of information is now being accumulated on linkage in corn and numerous scattered demonstrations of the phenomenon have been made in other organisms as well Only a rather simple explanation will be attempted here to bring out merely some of the fundamental principles of the phenomenon

When first considering Mendel s law the statement was made that more than one determiner might be located on a given chromosome As yet we have

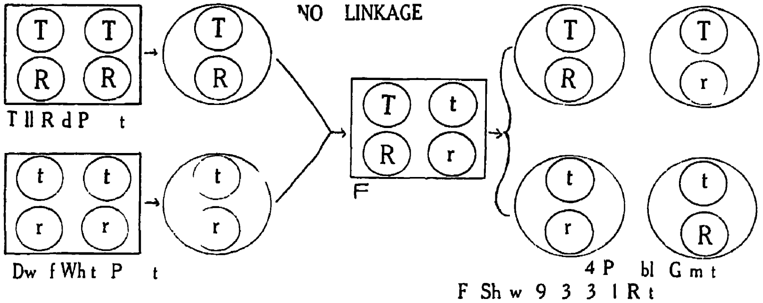


FIG 16—Diagram showing normal dihybrid behavior when no linkage is involved

considered no such case but linkage involves exactly this situation In connection with some of MENDEL S original crosses fig 16 will be recalled In this case a double dominant mates with a double recessive and the result is a dihybrid ratio in the F generation following the production of four types of gametes by the F plants Suppose however that the determiner *T* and the determiner *R* are carried on the same chromosome the situation would be as represented in fig 17 Here the I individuals produce only two types of gametes as in a monohybrid so that the F presents what amounts to a monohybrid ratio the tall individuals always being red flowered and the dwarf individuals always white flowered The results obviously arise from the fact that T and R are *linked* being located on the same chromosome as are also t and r

These linkage results taken by themselves might seem to recommend the following interpretation It is really the chromosome itself that is the important and indivisible unit in inheritance while the distinction

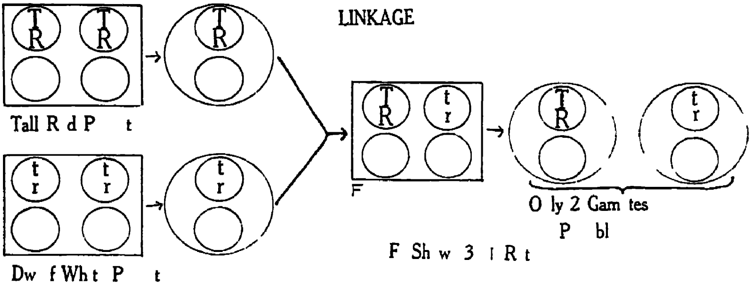


FIG 17—Diagram showing dihybrid behavior when enes are linked F produces only two types of gametes

between the various genes on a single chromosome is purely arbitrary and unnecessary In other words why need we assume that T and R are distinct genes when we would be equally justified in assuming that tallness and redness are merely two of the effects produced by the same chromosome? This latter assumption may appear attractive but it becomes clearly impossible when some of the further breeding results are considered

Following out the foregoing example (merely as an illustration) when it was discovered that tall individuals always had red flowers this fact was explained as linkage

The inference was that in these same cultures there could never appear a tall plant with white flowers nor a dwarf plant with red flowers for if there were linkage and the chromosome were the indivisible unit in inheritance it would be impossible for tallness and redness to become separated As a matter of fact it was soon recognized that these impossible individuals did actually occur Small numbers of tall whites and dwarf reds regularly appeared among the same cultures in which the linkage of tallness and redness had been demonstrated and the work had been done under such conditions of control that there could have been no experimental error

This new fact demanded an explanation for with such chromosomes as *TR* and *tr* it would be impossible to obtain a tall white individual so long as the individuality of the chromosome was maintained When chromosomes were examined with the modern lenses they were found to show all kinds of tangled contortions during the reduction division, and accordingly the scheme shown in fig 18 was devised These five stages represent phases that an allelomorphic pair of chromosomes may go through during reduction division This pair of chromosomes which would normally lie side by side (1) may at times come to lie across one another (2) In this position the middle regions of the chromosomes are in contact and are conceived of as fusing (3) The spindle fibers from each pole then lay hold of this compound chromosome and the pull comes in the direction of the arrows shown in the figure This results in the break indicated in (4) Finally two new chromosomes separate from the old compound chromosome as indicated in (5) Thus *T* becomes linked with *r* and later when a mating occurs between two gametes each of which contains such a chromosome the result is a tall white flowered

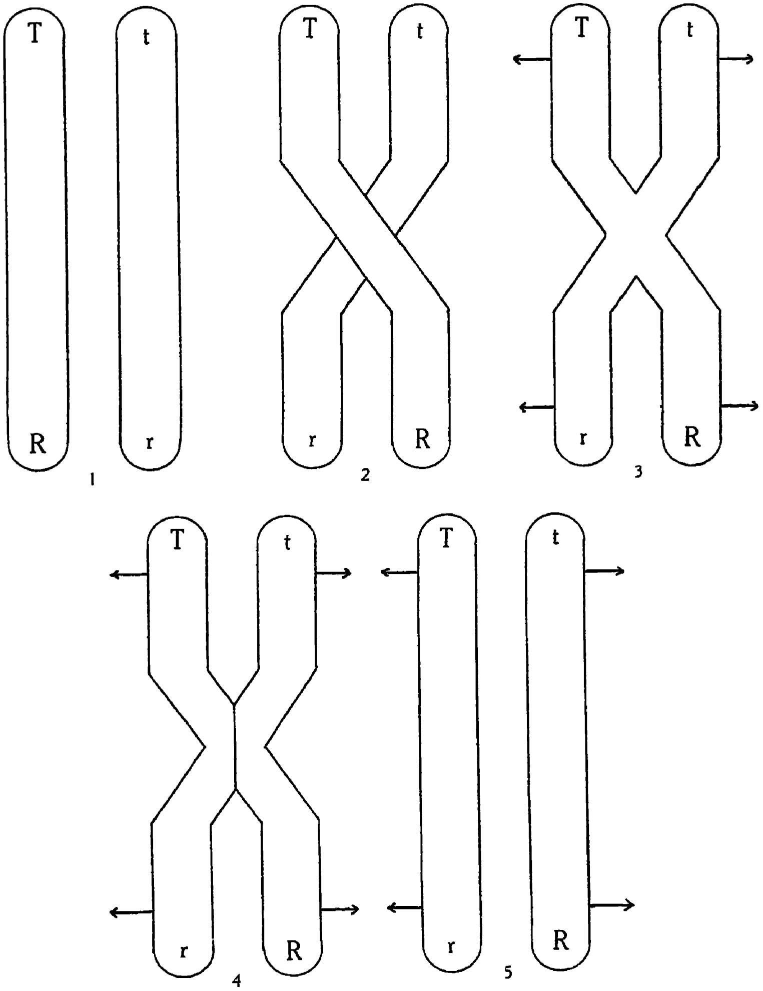
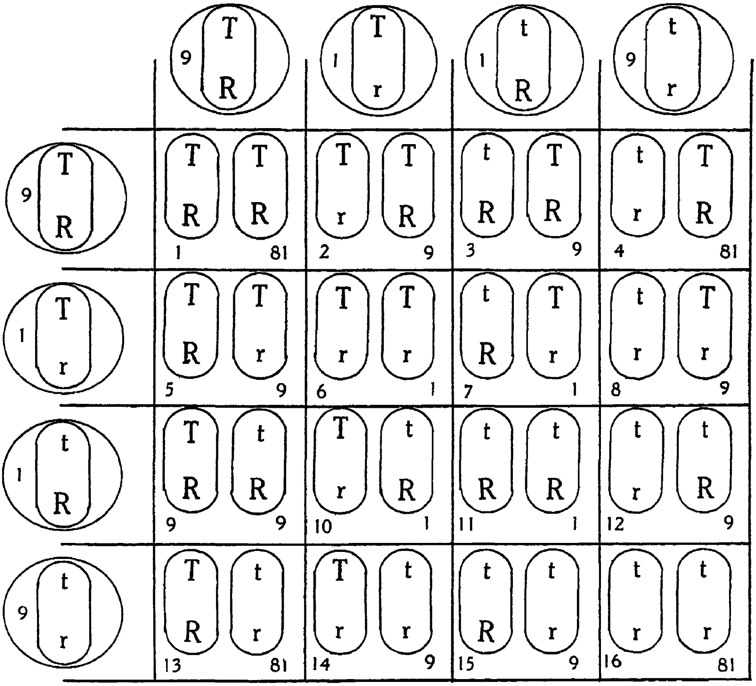


Fig 18 —Illustrating how crossing over may occur

individual In the same way and with equal likelihood dwarf red flowered individuals may appear

This scheme serves to account for the occurrence of the ' exceptional individuals in linkage cultures The whole phenomenon is known as *crossing over* It has been practically impossible to provide a direct demonstration that the chromosomes behave in exactly this manner during the reduction division but there has accumulated an enormous mass of indirect evidence from the breeding results to support this view Evidently the chromosome is not the indivisible unit in inheritance but is divisible according to a rather regular scheme Whole sections may be evenly exchanged between the members of an allelomorphic pair of chromosomes

Once the phenomenon of crossing over had been identified investigation was undertaken to determine the regularity and frequency of the phenomenon It was discovered that the amount of crossing over that took place between a given pair of genes had a constant value For example 10 per cent of the crossing over could be depended on to occur between *T* and *R* in every experiment involving these two determiners The exact cross over value is of course computed from the breeding results obtained In the present example a cross over value of 10 per cent between *T* and *R* would work out as follows In the reduction division (in the F hybrid which results from tall red×dwarf white) crossing over takes place in 10 per cent of the cases while crossing over fails and the original linkage relationships are maintained in 90 per cent of the cases As a result four types of gametes are produced in the following frequencies 45 per cent *TR* 45 per cent *tr* 5 per cent Tr 5 per cent tR or 9 TR 9 tr 1 Tr 1 tR The F population which results from the random matings among this assortment of gametes is represented in fig 19 the phenotypic ratio being 281 tall red 19 tall white 19 dwarf red 81 dwarf white In such cases of course the original investigator has for his data only this final pheno typic ratio and from these data must compute the amount of crossing over that has taken place In actual practice this computation would be simplified by the use of a formula As a matter of fact, the necessity of



	9 TR	1 Tr	1 tR	9 tr
9 TR	TR TR 1 81	Tr TR 2 9	tR TR 3 9	tr TR 4 81
1 Tr	TR Tr 5 9	Tr Tr 6 1	tR Tr 7 1	tr Tr 8 9
1 tR	TR tR 9 9	Tr tR 10 1	tR tR 11 1	tr tR 12 9
9 tr	TR tr 13 81	Tr tr 14 9	tR tr 15 9	tr tr 16 81

FIG 19 —Showing F population produced by random mating of gametes of F in a case of linkage with 10 per cent crossing over

using any such formula can usually be avoided through the following expedient Instead of inbreeding the F it can be back crossed with the double recessive parent (dwarf white) This parent race is perfectly homozygous so that it produces only the one type of gamete (in spite of crossing over which must be taking place here also) The results of this back cross are represented in fig 20 It is obvious that the phenotypic ratio obtained (9 tall red 1 tall white 1 dwarf red 9 dwarf

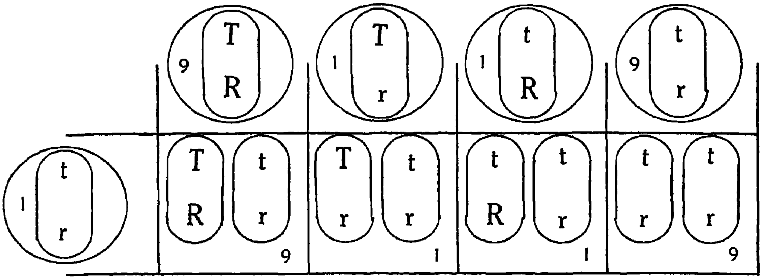


FIG 20—Population resulting from mating of gametes of F (shown above) with gametes of recessive parent (only one type of gamete shown at left) in a case of linkage with 10 per cent crossing over

white) corresponds exactly to the ratio among the types of gametes produced by the F In this way the cross over value is quite apparent and no computation necessary Back crosses with the recessive parent will always provide results which are easier to interpret than are the F ratios

As investigations were made of additional pairs of linked genes it was discovered that each such pair had a characteristic and rather constant cross over value For example assuming that a third gene *A* is located on the same chromosome with *T* and *R* by means indicated above a test is made as to the cross over value between *A* and *T* This value is discovered to be 20 per cent With these two cross over values determined consider able interest now becomes focused upon the relations of *A* and *R* Suitable tests reveal the fact that the cross over value between *A* and *R* is 30 per cent When three such cross over values as these are considered together MORGAN s theoretical scheme of the linear arrange ment of genes is immediately suggested for these results can best be interpreted on the following basis The genes are arranged in a line on the chromosome and the frequency of crossing over between any two genes depends upon their distance apart Using arbi trary units to correspond with the actual percentage of crossing over the three genes employed in the example may be arranged in the order *ATR* with *A* and *T* 20 units apart *T* and *R* 10 units apart and *A* and *R* there fore 30 units apart (The chromosome map first de vised e g fig 18 would then have to be modified some what to fit these new facts)

It is in this manner that MORGAN and his students have been able to construct rather startling chromo some maps indicating in a very exact way the relative position and spacing of scores of genes on a single chro mosome Striking confirmation of the scheme appears in the following fact The fruit fly possesses four chro mosome pairs one of which is visibly much shorter than the others Breeding results reveal that the many known genes are associated in just four linkage groups one of the four groups containing a much smaller number of genes than the other three and being distinctly shorter as mapped from the cross over values In truth this scheme of MORGAN S has such an enormous mass of data to support it that for all practical purposes it may be regarded as an established fact

Cross over values in the fruit fly may run as high as 80 per cent and in one of the related species much higher values have been reported (LANCEFIELD 4) Such a high cross over value seems rather surprising for it represents a case where the cross overs are much more frequent than the non cross overs It should be realized that a cross over value of 50 per cent where cross overs and non cross overs are equally frequent would give exactly the same breeding results as if the two genes in question were located on different chromosome pairs Similarly cross over values higher than 50 per cent would give the same breeding results as though the linkage were reversed that is if *M* and *N* were 80 units apart the breeding results of a single experiment involving *M* and *N* only would seem to indicate that *M* was linked with *n* and *m* with *N* It is evident therefore that these higher cross over values are computed from a considerable set of experiments Every newly discovered gene is carefully tested with at least two other genes whose position is already known and thus the new gene is accurately placed on the chromosome

The cases that have just been discussed are known as single cross overs the two chromosomes of the pair come to lie across one another at a single point and a single break with the subsequent rearrangement is sufficient to account for the results In view of the physical mechanism which seems to be responsible for these cross overs it is not surprising to find that there may sometimes occur double cross overs In these cases the two chromosomes come to lie across one another at two points and a break takes place at each point with the corresponding exchange of chromosome regions This amounts to an even exchange of corresponding zones from the middles of the chromosomes with the two end zones on each chromosome remaining as before Inasmuch as crossing over of any sort is detected only through its effect on the breeding results double crossing over can be demonstrated only in experiments that involve observations on at least three genes that are rather widely separated on the same chromo some As would be expected double cross overs are much less frequent than single cros overs There have also been reported very rare cases of triple cross overs

The question arises whether the frequency of crossing over depends strictly and only upon the real distances between the genes on a chromosome In the first place it is theoretically possible that certain regions of a chromosome may owing perhaps to physical peculiarities lend themselves more readily to crossing over than do other regions of the same chromosome (A suggestion to this effect appears in some of MULLER s work see chapter on Mutation) This possibility is of necessity ignored in the chromosome maps which are constructed purely on the practical assumption that crossing over is proportional to distance In the second place it is recognized that certain special influences such as temperature and age of the organism may modify the normal frequency of crossing over Dependable values on crossing over are to be obtained therefore only when such conditions are absolutely standardized (STURTEVANT 6) Further one of the outstanding and unexplained peculiarities of this phenomenon is that in the fruit fly crossing over takes place freely in the female while none whatsoever takes place in any of the chromosome pairs of the male It is interesting to note that in organisms where the female is heterozygous for sex—female homozygous for sex in the fruit fly—exactly the reverse is true crossing over taking place in the male but not in the female (TANAKA 7) In corn where both sexes are represented on the same individual there is no such restriction for crossing over takes place with approximately equal frequency in microsporogenesis as in megasporogenesis (EMERSON and HUTCHINSON 3) Finally it has been demonstrated that the presence of certain pecial genes will modify the frequency of crossing over so that it has been possible to isolate races of the fruit fly in which an extremely high or an extremely low rate of crossing over takes place (STURTEVANT 6 DETLEFSEN 1)

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CHAPTER VII

MUTATION

When DE VRIES discovered the phenomenon of mutation in *Oenothera Lamarckiana* he stated that mutations were qualitative discontinuous constant changes in the germ plasm (see p 6) These three fundamental characteristics still hold true but some of DE VRIES other ideas have been considerably qualified by later work The critical analysis of the germ plasm that has been effected during the last decade has made it possible to describe mutation in a much more exact way than before and to describe it in terms of the Mendelian mechanism

For convenience our discussion of this general subject will be put into the form of a classification (The sequence followed in this classification is that of the increasing magnitude of the area of the germ plasm affected by the change)

I GENE CHANGES

1 LOCUS CHANGES —These are changes restricted to a single locus of one of the chromosomes so that they involve only one gene without affecting even its nearby neighbors Usually they are effective on only one chromosome of a pair without affecting the corresponding locus of its allelomorphic mate Consequently the change first appears in the heterozygous condition (BAUR estimates that such changes originate in the heterozygous condition four hundred times as frequently

as in the homozygous) They are mostly loss mutations and recessive to the previous condition Only a very few dominant or gain mutations have ever been reported

Baur (1) working with *Antirrhinum* concludes that changes of this sort take place more frequently in the vegetative tissues than in connection with gametogenesis The earlier work on the fruit fly indicated that the locus changes took place late in gametogenesis since only one individual of the new type would appear in a progeny Later investigation however has indicated that the change may take place at almost any point in ontogeny (Bridges 4, Muller 8) (There are also indications that changes of this sort may take place in purely somatic tissue although in such cases of course the modification cannot be perpetuated See also chapter viii on this matter)

Zeleny (12) states that there is no periodicity to these mutations thus refuting one of the early ideas of De Vries The same investigator demonstrates that reverse mutations are more frequent than original mutations (This however is simply because they are in the reverse direction and not because of their recent origin) In the case of these reverse mutations the changes are always full jumps back to the original starting point and never result in an intermediate condition nor will the selection of extreme types at all modify the rate at which these reverse mutations occur

Muller and Altenburg (10) who have conducted a critical examination of the fruit fly for mutations occurring on the first and second chromosomes state that the vast majority of locus changes have a lethal or semilethal effect when present in the homozygous (recessive) condition (It is obvious therefore that a critical search for these mutations must involve a very special technique These authors are in possession of such a technique through their intimate knowledge of the linkage groups on the chromosomes in question and their ability to detect the absence of certain expected classes) On one chromosome they uncovered the startling fact that 50 per cent of the mutations were located in a restricted region at one end of the chromosome which amounted to about 2 per cent of its length as charted from cross over values (It is an open question whether this indicates a highly mutable region of the chromosome or whether cross over values are an inaccurate index of length)

The most promising phase of Muller s work arises from his critical study of the rate of mutation Considering the whole length of the first chromosome of the fruit fly one mutation occurs in 106 gametes For the second chromosome the corresponding value is one in 175 gametes Zeleny states that locus changes occur as frequently in one sex as in the other Having established these constants Muller is now investigating the possibility of modifying the normal rate of mutation Already he has been successful in depressing the rate one half by means of low temperatures Eventually such knowledge may be turned to some practical value

Two further points should be mentioned about the locus changes Variation of this type has been encountered (or at least identified) much more frequently than have any of the other types of changes mentioned below The term mutation is usually restricted by geneticists to apply to locus changes

The presence and absence hypothesis has been very generally accepted because of its value in simplifying our concepts and providing the most convenient scheme of notation At the same time it is recognized that this hypothesis may not strictly represent the truth in all cases There are two outstanding types of evidence that can hardly be interpreted by means of the presence and absence concept One of these will be discussed later in another connection (p 151) The other is as follows

In some cases other possibilities may be realized in connection with a single locus than merely the presence or absence of a given gene For example at a given locus on one of the chromosomes in corn a condition *W* may exist which results in colorless pericarp In other plants that same locus may bear the gene *V* variegated pericarp and in still others *S* completely colored pericarp *S* is dominant to *V* and *V* to *W* (see also p 119) As a matter of fact these three are simply representatives of a series of ten different conditions that may be present at a given locus Such cases are spoken of as systems or series of *multiple allelomorphs* and it would be difficult to harmonize them strictly with the presence and absence hypothesis

The relation of systems of multiple allelomorphs to mutation is significant It would be possible to arrange the genes involved in any system of multiple allelomorphs in a series placing at the top the one which was dominant to all the others and at the bottom the one that was recessive to all the others This series however in no way reflects the order in which such genes have originated by mutation In the fruit fly there is a famous series of multiple allelomorphs for eye color ranging from white through progressive steps in intensity of coloration but it is not true that white first mutated to a light shade which later mutated to the next darker shade and so on nor is it true that this series of mutants came off in a regular sequence down the scale of color intensity In short within a series of multiple allelomorphs the mutants come off in discontinuous rather than continuous series It follows that mutations cannot be led along in a given direction by means of selection

Further although it is common that all the genes in a series of multiple allelomorphs affect the same general character exceptions to this have been noted MULLER (9) cites a case in which the different mutant genes at the same locus may cause either shortening of wing eruption on thorax or a lethal effect

At the same time although we are thus repeatedly encountering evidence on the discontinuity of mutation it is possible that there is an underlying continuity of a sort that we are not in a position to measure A statement of MORGAN s (6) bears on this point Evidence is fast accumulating that common genes probably undergo analogous mutation in related species the direction being conditioned by the physico chemical constitution of the gene and not by some hypothetical directive force

2 COMPLEXMUTATIONS —It is perhaps surprising that in spite of the numerous cases of locus changes that were being discovered there were for a long time no clear cases of mutations involving simultaneous changes in several neighboring factors in one region of a chromosome NILSSON EHLE (11) now claims to have such a case and calls it complexmutation Normal wheat mutates to bearded speltoid involving a simultaneous change in two closely linked genes Among the F progeny of normal × mutant appear a few bearded normal type and beardless speltoid but only a few due to the very close linkage of the two mutated genes In another case the same investigator claims that three linked factors have mutated simultaneously

3 DEFICIENCY —A rare phenomenon has been described by BRIDGES (3) working on the fruit fly Deficiency as he calls it is something more extensive than a simple locus change (and probably more extensive than the complexmutations) It is a regional mutation involving an inactivation of a portion of a chromosome so that the genes on that region of the chromosome are rendered ineffective (nor can crossing over take place in that region)

II CHROMOSOME CHANGES (CHROMOSOME ABERRATIONS)

1 DUPLICATION —BRIDGES (3) describes another rare type of change in the germ plasm to which he gives the name duplication Judging from the very unusual breeding results obtained some abnormality in connection with mitosis has resulted in the

appearance of an extra piece of chromosome which duplicates in its gene content a known region of one of the normal chromosomes An organism in this condition is really triploid with respect to a part of one of the chromosome sets

2 NON DISJUNCTION —This phenomenon made famous through the classic work of BRIDGES on the sex chromosomes of the fruit fly (chap XIII) may prove to be a fairly common occurrence In an irregular reduction division one of the chromosomes fails to disjoin properly from its mate As a result one or two gametes are formed with an extra chromosome and others which lack this chromosome The latter fail to function but a mating of the former with a normal gamete would produce a zygote with an extra chromosome BLAKESLEE BELLING and FARNHAM (2) have discovered this phenomenon in the jimson weed *Datura* The normal diploid number of chromosomes in this form is twenty four Twelve different mutants have been discovered with twenty five chromosomes each This seems to indicate that each of the twelve chromosomes (haploid) has failed to disjoin at least once in history These twelve new forms are abnormal in their vegetative features notably low in fertility and tend to revert to the normal diploid ancestor

3 TETRAPLOIDY —A hurried or incomplete mitosis will sometimes result in the simultaneous duplication of all of the chromosomes This phenomenon has been observed several times in culture and there are indications that it has taken place frequently in the past A general survey of the chromosome counts in our existing plants and animals emphasizes the fact that the haploid number is much more frequently an even number

than an odd one This together with the fact that there are several species groups in which the chromosome count of some of the members is just twice that of the others suggests that tetraploidy may have played a considerable role in evolution Tetraploidy commonly but not always brings gigantism

BLAKESLEE now puts the finishing touches on this tetraploidy conception by more work on *Datura* In addition to the abnormal forms with twenty five chromosomes he has discovered one completely triploid (thirty six chromosomes) and one tetraploid form (forty eight chromosomes) These latter both seem to be in a better balanced condition than the non disjunctional (twenty five chromosome) forms since they are more normal with respect to their vegetative features and fertility

The beauty of the situation arises from the fact that the tetraploid type contains a previously known Mendelian factor In normal diploid forms a hybrid of the composition *Aa* will give a 3 1 ratio of purple flowered and white flowered in the F The tetraploid hybrid *AAaa* gives gametes in the ratio 1 *4 4* 4 *A 4* 1 *aa* Chance matings among these results in an F of 35 purple 1 white The F_3 and later generations behave according to expectations on this basis

As stated before the term mutation is now commonly restricted to locus changes The author has not discovered the conventional term to include all of the foregoing cases unless it be merely germinal variations

The bearing of these phenomena upon evolution might be considered briefly Until a few years ago the general belief on evolution included the following notions inheritance of acquired characters has been exploded Darwinian variations are rather dubious as a basis for explaining evolution but mutation with natural selection among the mutants will doubtless account for most of the facts Now in view of the more accurate knowledge of the mutation phenomenon that has been developed in recent years the adequacy of mutation in explaining evolution must be considered more critically

First of all it is evident that complex mutation deficiency and duplication could have played no important part in evolution merely on account of the extreme rarity of these phenomena if for no other reason Locus changes are sufficiently common but consider the quality of the mutants which result! In practically all cases the change is a loss mutation and surely evolution cannot be accounted for on such a basis! One might merely regard this as evidence of the trial and error method by which nature operates only rarely making those gains which must serve as the basis of progressive evolution A few gain mutations have been reported but there is reason to suspect that even these may be merely reverse mutations regaining that which had previously been lost Furthermore the locus changes that have been reported be they losses or gains have seemed consistently non adaptive In short it is difficult to imagine how progressive evolution can be accounted for either through single locus changes or through the accumulation of numerous locus changes One can readily admit that such changes may account for the multiplication of varieties or even species on the same level but can hardly be convinced that our larger phylogenetic edifices have been erected from such building blocks It is quite likely however that our knowledge is still too limited to visualize the evolution of the ages in terms of what we have seen happening during a very few years

Non disjunction is out of the question as a basis for evolutionary progress The resulting unbalanced forms are clearly abnormal and it is very doubtful whether they could permanently perpetuate themselves under the most favorable conditions much less survive under conditions of sharp competition and environmental stress

Tetraploidy might well account for a certain amount of evolutionary progress and we have good evidence that it has actually done so in the past The tetraploid form has more doses of desirable growth factors than had its diploid ancestor and as a rule is visibly more vigorous in one respect or another A theoretical limitation however applies here also Tetraploidy involves merely a quantitative gain a multiplication of genes already present One feels that not much progressive evolution could take place without the appearance of qualitatively new gene and the production of distinctly new adaptive characters

It would be safe to state that the foregoing considerations have caused many biologists to feel less certain in explaining evolution than they were a few years ago This loss of faith in mutation taken together with recent discoveries on inheritance of acquired characters (see chap ii) is causing many to seek an explanation of progressive evolution in Lamarckian terms

It is of some interest to note that the original classic examples of mutation provided by DE VRIES are probably not genuine cases It had long been suspected by some that *Oenothera Lamarckiana* was a hybrid and its mutants merely extracted recessives but it was difficult to account on this ba is for the very small number of mutants that were thrown every generation MULLER (7) probably deserves the credit for solving this vexing problem In the fruit fly he discovered an essentially true breeding hybrid race and explained it by a system of balanced lethal factors These factors assert their lethal effect only when they occur in the homozygous recessive condition In thi race of flies two such factors are present in heterozygous condition on the same pair of chromosomes the dominant members of the heterozygous sets being on the opposite chromosomes of the pair Such a hybrid continues to breed true as such since any attempt to segregate brings the homozygous recessive condition of one or the other lethal with resulting death to the progeny The recessives of any heterozygous set of genes on this same chromosome pair will remain concealed when this stock is allowed to inbreed Occasional crossing over will cause the appearance of a few of these recessives (in predictable frequencies) like the mutants thrown by *Oe Lamarckiana*

In fact DE VRIES himself now subscribes (5) to an explanation fundamentally similar to the preceding About one half of the seeds of *Oe Lamarckiana* are empty DE VRIES explains this by saying that *Lamarckiana* produces two kinds of gametes the typical or *laeta* and the *velutina* Each gamete has a lethal factor closely linked with the character factor Heterozygous combinations give good seeds homozygous give sterile If one of the two lethal factors becomes vital the *Oe laeta* or *Oe velutina* mutation appears

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CHAPTER VIII

BUD VARIATION

The outstanding feature of bud variation is that we know very little about it It is true that quite a number of cases of bud variation have been investigated but it could hardly be said that altogether satisfactory explanations of the phenomena have as yet been provided The relation between bud variation and the Mendelian mechanism is difficult to visualize with much clearness nor is it easy to interpret the various cases in terms of each other

Bud variation may be defined as variation originating in vegetative tissue Such variation might involve merely (1) fluctuation a response to environmental stimulus or it might involve (2) a change in the genetic constitution of the parts affected Cases of type (1) need not concern us here since such variations are not inherited As for type (2) this should be subdivided into (*a*) cases in which the variation involves both somatic and germinal tissue and in which therefore the variation will be heritable through seed and (*b*) cases in which the variation involves somatic tissue alone the variation not being heritable through seed With these distinctions in mind we may consider a classification of the phenomena of bud variation which is based primarily upon the ideas of EMERSON (6)

I SOMATIC MUTATION OF GENES

This may be illustrated by some of the findings of EMERSON in corn An illustration of variation involving both somatic and germinal tissue is provided by the behavior of pericarp color *S* is a gene which results in self (completely) colored grains being dominant to *V* which produces variegated grains and which in turn is dominant to *W* which produces colorless grains (These are three members of a series of multiple allelomorphs see p 112) Corn of the formula *VW* and which should therefore have all the grains variegated will at times have some grains that are self colored Further breeding reveals that somatic mutation has occurred in the tissues concerned with the formation of these grains such that *VW* has become *SW* The change has taken place not only in the somatic tissue of the grains in question but also in the germinal tissue within the grains and is inherited accordingly It is concluded that the recessive variegation gene *V* has mutated to its dominant self color allelomorph *S*

Without attempting a discussion of the breeding tests upon which EMERSON based his conclusions it will be worth while at least to mention some of the other peculiarities of this phenomenon *V* mutates to *S* rather frequently but *W* never mutates to *S* *V* in the heterozygous condition (*VW*) mutates to *S* five times as frequently as when it is in homozygous combination (*VV*) The mutation takes place late in ontogeny much more often than in early ontogeny As a result there are many more cases where small patches of self colored grains appear on variegated ears than where large patches appear In corn of the *VV* formula only one of the *V* genes ever mutates to *S* at a given time Reverse mutations *S* changing to *V* have also been noted

This same material provides also an example of somatic mutation which involves the soma alone and not the germinal tissue In situations essentially similar to those described above there may appear on the variegated ears a few aberrant grains which are apparently self colored only on the crown of the seed This character has been designated as dark crown and it is notable that it is never inherited Microscopic examination of the dark crown and of the fully self colored seeds indicates that in the former the epidermis alone is colored while in the latter the epidermis alone remains colorless The conclusion seems warranted therefore that the two types of variation are fundamentally the same both being true gene mutations and that the non inheritance of the dark crown type is due to the accident that it occurs in the epidermal tissue outside the germ tract

II SOMATIC SEGREGATION

It has been pointed out by several investigators that bud variations appear much more frequently in plants that are heterozygous for the genes concerned than in plants which are homozy gous This may be true but it would not be safe to conclude that there is any mechanism ever provided in somatic tissue which corresponds to the normal Mendelian mechanism for segregation during gametogenesis If somatic segregation ever takes place it is through the operation of some quite different mechanism as indicated in the examples given below

1 CHROMOSOME ELIMINATION —A theoretical illustration would be as follows A plant heterozygous for linked genes *A B* *a b* has an irregular mitosis take place in some part of its somatic tissue One of the daughter nuclei of this mitosis fails to receive its full complement of chromosomes the *A B* chromosome having somehow been eliminated This cell and its progeny haploid now with respect to this chromosome pair which is represented only by the *a b* chromosome will form tissue in which the recessive characters *a* and *b* will become manifest

This would be the principle underlying somatic segregation through chromosome elimination As a matter of fact there are really only two clearly demonstrated cases of this sort and both of these are limited to rather special situations In one of these cases gynandromorphism in the fruit fly a special chromosome set is involved the sex chromosomes This will be taken up therefore in the chapter on Sex determination In the other case endosperm mosaics in corn a special triploid tissue the endosperm is involved This case will be discussed in the chapter on The endosperm in inheritance

2 CHIMAERAS —A chimaera is a plant in which some of the tissues have all of the characteristics of one variety or species while the rest of the tissues on this same plant are characteristically those of a different variety or species The most famous chimaeras are the graft hybrids of *Solanum* produced by Winkler (10) This investigator made grafts of two distinct species of this genus the tomato and the nightshade After the tissues of stock and scion had been given time to weld together Winkler cut the stem in such a way that the exposed cross section was made up partly of tissues of the stock and partly of scion tissues From this cut surface adventitious buds would arise and at times these buds came at the exact point where stock and scion tissues were in contact Such buds developed branches which

were *sectoral* chimaeras the tissues of one side of the branch being those of the tomato while the tissue of the other side of the branch were night shade tissue Such sectoral chimaeras would not infrequently later produce branches that were *periclinal* chimaeras having the tissues of one species inclosed within an envelope of the other That these were really periclinal chimaeras was established by chromosome counts (tomato and nightshade having different chromosome numbers) and by the fact that seedlings produced by them were always of the species of the subepidermal tissue from which the gametes arise The periclinal chimaeras in turn were observed at times to produce branches wholly of one or the other of the parent species a performance which may well be regarded as a type of somatic segregation

Fundamentally the same behavior has been observed in certain natural periclinal chimaeras (notably in types of *Pelargonium* BAUR 2) involving white (deficient in chlorophyll) and green tissues The manner of origin of these natural chimaeras is unknown but it is quite possible that they arose as somatic mutations

A very interesting case has been reported by BATESON (3) in *Bouvardia* which presumably may be something of the same sort as the foregoing Varieties of *Bouvardia* that are maintained true to type by propagations from stem cuttings produce plants with very different flower form size and color when propagated by root cuttings Since in normally produced buds of the stem both the epidermis and the deeper lying tissues are maintained through direct cell lineage while the roots produced by stem cuttings arise from the plerome and break through the periblem and dermatogen forming these parts anew sprouts that develop from the roots must have the genotype of the stele rather than that of the cortex or epidermis

It is clear that classes 1 and 2 represent distinct types of somatic segregation the first arising as the result of irregular chromosome distribution and the second from a segregation on the part of tissues as a whole Both might well be regarded as anomalies since they are to be explained by irregularities in the common plant program There remains to be considered one more type of somatic segregation and here although no such finely balanced mechanism for segregation is involved as that of the reduction division at least the segregation is effected with some regularity

3 CYTOPLASMIC SEGREGATION —Numerous cases of apparent segregation of cytoplasmic elements have been provided in plants All of them involve visible effects on chlorophyll and all show non Mendelian inheritance (Cytoplasmic segregation is the concluding item in EMERSON s classification of bud variation In order better to bring out the relationship between cytoplasmic segregation and certain other plant phenomena this item will be taken up as a part of the following classification [from WINGE 9] of cases of chlorophyll inheritance)

CHLOROPHYLL INHERITANCE

I Mendelian inheritance the characters being carried in the nucleus

Quite an array of case of chlorophyll deficiency have been found to be inherited according to the normal Mendelian mechanism In this class have been noted albino pale green yellow and variegated types which are (usually) inherited as imple Mendelian recessives to the normal green condition

II Non Mendelian inheritance the characters being carried in some extra nuclear portion of the gametes (EMERSON S cytoplasmic segregation)

1 Biparental inheritance the male as well as the female parent contributing (presumably) both cytoplasm and plastids to the zygote

A The chlorophyll character governed by the distribution of the plastids themselves

An example of this type of thing is provided by the work of BAUR (2) on certain types of *Pelargonium* where the following behavior has been noted If a white leaved plant (white leaved branch see below) and a normal green leaved plant are crossed (either way) the resulting hybrid illustrates what has been called by some particulate inheritance that is the hybrid is variegated showing irregular patches of green and white If one of these white patches completely includes a bud there will probably be produced by that bud a completely white branch The flowers of this branch when self fertilized give rise through their seeds to white individuals only and would evidently continue to breed true to the white condition if white individuals could be matured In like manner the variegated hybrid may give rise to a pure green branch which would start a line of pure green individuals

A suggested explanation of this situation is that the white condition results from the occurrence of purely colorless plastids in the tissue while the green condition has the normal green chloroplasts A cross between the two types will introduce into the hybrid zygote a mixture of green and white plastids (plastid primordia) and the same result will be obtained whichever way the cross is made since the male as well as the female parent contributes plastids to the zygote During somatogenesis in the plant which develops from such a zygote there will be an inevitable segregation of green and white plastids since there is no mechanism provided for a perfectly even distribution to daughter cells of those cell components which lie outside the nucleus If the number of plastids per cell be not too large sooner or later through the operation of the laws of chance cells will arise which contain plastids entirely of one sort or the other and these will produce tissues which are pure green or pure white

B The chlorophyll character governed by the distribution of other and finer cytoplasmic elements than the plastids themselves

Again male and female parents both contribute the effective extra nuclear elements to the hybrid zygote and again a tendency toward irregular segregation appears during somatogenesis of the resulting plant In this case however the effective units are so small and numerous that a complete segregation of units of the two types is never achieved but merely the production of relatively paler and relatively greener regions on the plant

The behavior of IKENO s (7) *albomaculata* type of *Capsicum* might be interpreted on this basis Paler and greener patches occur on the *albomaculata* plants and the average paleness of the whole individual may be greater or less Since this average paleness of the parent is reflected in the nature of the offspring from any sort of a cross it is felt that such a parent produces gametes having a characteristic proportion of green and white elements or units whatever these elements or units may be

2 Maternal inheritance the male parent contributing only a nucleus to the make up of the zygote

In cases of this sort the source of pollen makes no difference so far as the chlorophyll character is concerned Consequently since this maternal inheritance cannot be accounted for by parthenogenesis in the plants that were used it has been concluded that the seat of the character in question is in something that the female parent regularly contributes and the male parent never contributes This idea is supported by certain cytological evidence that suggests the fact that in some plants at least the male nucleus is stripped clean of its cytoplasm at the time that it is discharged from the pollen tube into the embryo sac A similar distinction to that made under 1 may also be applied here

A The chlorophyll character governed by the distribution of the plastids themselves

It follows that pure green and white parts will at times segregate out in the variegated plants concerned CORRENS (5) *albomaculata* type of *Mirabilis* is said to be an example of this sort of thing

B The chlorophyll character governed by the distribution of other and finer cytoplasmic elements than the plastids themselves

It follows that absolutely pure green and pure white parts will never segregate out but only relatively paler and relatively greener parts WINGE (9) cites some of his own work on a variegated type of *Humulus* as an example

In conclusion it should be said that opinion as to the seat of chlorophyll inheritance is by no means settled It would doubtless be wise to regard the foregoing classification of WINGE'S merely as a convenient form in which to arrange the available evidence other investigators would certainly disagree with some of WINGE'S interpretations of the phenomena

As an example of a case which can hardly be forced into WINGE'S classification ANDERSON'S (1) green and white variegated race of corn might be cited Inheritance is strictly maternal and pure green and white areas segregate out on the leaves Presumably then this would fit into WINGE'S class II A But a careful cytological investigation of this material by RANDOLPH (8) has revealed that there can be no sharp segregation among green and white plastids at play to account for the green and white areas that it must be rather a matter of the general physiological condition of the two types of tissue It is interesting to note that in this case a type of somatic segregation occurs on the ear of the variegated plant resulting in certain *groups of seeds* that will produce green seedlings other groups of seeds that will produce white seedlings and still other groups of seeds that will produce variegated seedlings

In short the cases of chlorophyll inheritance on a non Mendelian basis are still under considerable discussion a perfectly clear interpretation of the phenomena is not as yet available Of this much however we may be sure there is such a thing as non Mendelian inheritance and it becomes manifest in connection with a type of character which on other occasions is inherited according to the normal Mendelian scheme In any event such cases should not be regarded as a violation of Mendel s law but merely as something outside the scope of Mendel s law since they are evidently transmitted by some extra nuclear mechanism

In good part the known examples of non Mendelian inheritance are limited to such cases of chlorophyll inheritance as have been cited above There is another small group of cases however that must also be regarded as illustrating non Mendelian inheritance although in quite a different way BATESON and his coworkers (4) have discovered certain instances (e g inheritance of doubleness in *Matthiola*) in which the male and female organs of the same plant differ in the factors they carry A clear explanation of this phenomenon has not been provided but whatever the explanation may turn out to be it seems certain that it will provide an exception to the normal Mendelian mechanism Such cases have led BATESON to suspect that plants as genetic machines differ fundamentally from animals segregation being clearly connected with synapsis in animals but not always in plants This difference in the machinery may be tied up with the fact that in animals the rudiments of the gametes are often visibly separated at an early embryonic stage whereas in the plant they are given off from persistent growing points

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CHAPTER IX

THE GAMETOPHYTE IN INHERITANCE

Thus far the discussions have dealt with inheritance in sporophytes in fact genetics practically never considers gametophytes through which inheritance must pass from one sporophyte to the next The reasons for this neglect are obvious Practically all of our land vegetation is made up of sporophytes and therefore practically all of our experimental material has been sporophytes Furthermore gametophytes are inconspicuous (out of sight in seed plants) hard to get at hard to work with and apparently of no economic importance Besides in animals as is well known the generation equivalent to the gametophyte of plants is represented by only a few cell divisions in the maturation of gametes In other words the gametophyte has no significance as a discrete generation in the animal kingdom and since inheritance in plants is of interest to the public chiefly because it throws some light upon inheritance in animals there has been little demand for any knowledge of inheritance in gametophytes

It is not surprising therefore that very little study has been made of the gametophyte generation in inheritance There are reasons for believing however that such a study might be very profitable The gametophyte generation with its haploid chromosome number would provide an interesting and critical test of the Mendelian mechanism of inheritance Certain features of inheritance would be expected to differ radically from inheritance in sporophytes A generalized example might be considered

Gametophyte *Ab* is characterized by exhibiting the *A* character but not the *B* The reverse is true of gametophyte *aB* A cross between the two would produce zygote *AaBb* followed by a sporophyte of the same formula The following gametophyte generation would contain four types in equal numbers *AB* *Ab* *aB* and *ab* This is the program that would have to be followed if the Mendelian mechanism were at play One would expect there fore that there would be the following outstanding characteristics of inheritance in gametophytes (1) There could be no possibility of dominance since but one representative of an allelomorphic pair could be present Any discovery of blending inheritance in gametophytes (with respect to a monohybrid situation) would serve to cast doubt upon the Mendelian mechanism (2) Clear segregation would appear in the first generation following the cross and the phenotypic ratios would be quite different from those encountered among sporophytes The various factor types might of course be expected to operate but again the ratios obtained would be unusual All of this however is little more than idle speculation serving merely to point out discoverie that might be expected in the future

A study of inheritance in gametophytes might be profitable for other reasons also Among those higher plants which have been the objects of genetical research the sex act is a very well insulated performance occurring deep within the tissues Furthermore it is both prefaced and followed by quite a sequence of events which we know must be taking place with considerable regularity but which we cannot control Surely there would be much greater hope of any artificial manipulation of the sex act making possible a more critical study of the germ plasm in those organisms where the gametes themselves could be manipulated It would seem that such things might be possible in those lower plants where the gametophyte is the dominating generation although the technique necessary for such experiment would doubtless be difficult to develop

The actual work that has been done on inheritance in gametophytes is practically nil Pure line studies have been made in a number of thallophytes selection has been attempted and some mutations have been found but none of the experiment has revealed anything critical on the matter of segregation of characters following a sex act

TRANSEAU (2) has made some observations on the green alga *Spirogyra* which while they did not involve any experimental work were nevertheless quite suggestive This author was familiar with several species of *Spirogyra* in their natural habitats and noted several natural populations which were clearly mixtures of two or more different species Under such circumstances filaments of one species were observed in the act of crossing with filaments of another species Furthermore in such mixed populations there were discovered some filaments which were evidently the products of previous crosses for they clearly showed new combinations of the characters of two species It is to be hoped that exact experimental work will prove feasible with this genus

One instance of the clean segregation of characters in the gametophyte generation is to be found among angiosperms Belling s semi sterility among beans This will be described later in the discussion of the general subject of sterility For the most part the gametophyte of angiosperms seems to be merely an expressionless intermediate stage between succeeding sporophyte generations As East (1) puts it Modern discoveries tend more and more to show that the sole function of the gametophyte of the angiosperms is to produce sporophytes The characters which they carry appear to be wholly sporophytic the factors which they carry functioning only after fertilization

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CHAPTER X

STERILITY

The subject of sterility in plants is only in part a matter of genetics Many of the problems involved can be solved only by the physiologist ecologist or cytologist Some phases of the subject however have been rather successfully interpreted in terms of genetics Tentative outlines of the general subject will be presented merely to show what parts of the problem are being attacked by the geneticist

First of all sterility might be classified in terms of the effects produced

A Sterility Complete failure of the sex act

B Semi sterility Failure of part of the pollen or part of the ovules or part of both

C Self sterility Pollen and ovules functional in cross fertilization but not in self fertilization

A more comprehensive classification might then be arranged on the basis of cause although such a classification in our present state of knowledge must be rather vague and uncertain

I Environmental causes (Merely a few examples will be indicated This part of the subject properly belongs to the ecologist and physiologist)

The examples of environmental causes given below commonly result in complete sterility A although under special circumstances situations corresponding to B or C might be set up

1 Conditions too moist

When species that have become adapted to relatively dry conditions are subjected at the time pollen is mature and shedding to unusually moist conditions the pollen grains may absorb enough moisture to swell up and burst prematurely thus losing their usefulness (The sex act might also be circumvented by hard rain coming immediately after pollen distribution which would wash the pollen grains off the stigmas and thus result in a certain amount of sterility)

2 Conditions too dry

Unusual drought at the period that the stigmas are receptive may dry the stigmatic surfaces to such a degree that pollen grains will not adhere and germinate Conditions of this sort at times limit the setting of seed in such plants as corn

1 and 2 provide an illustration of a principle which is frequently encountered in biology—opposite extremes of conditions bringing a similar end result (although the intervening sequences of causes and effects will of course differ) Other illustrations of this same thing appear later in this classification

3 Poor nutrition

This may so limit the development of plants that they fail to mature up to the point of effecting a sex act

4 Good nutrition

A principle familiar to botanists is that the optimum growth conditions frequently maintain the plant in the purely vegetative phase so that reproductive parts are not developed (The plant physiologist describes this in terms of a carbohydrate nitrogen ratio)

5 Season too short

Plants adapted to a long growing season are unable to complete their normal life cycle up to the point of successful reproduction when grown in regions which have a short season

6 Unusual light conditions

Flowering and fruiting of many kinds of plants is induced by exposure to specifically favorable length of day which varies widely with the species (see ALLARD and GARNER 1) Radical departures from the customary seasonal program in this matter may serve to inhibit flowering and fruiting (It may be that the underlying causes involved here are similar to those of 3 and 4)

Other examples of environmental causes for sterility could doubtless be provided by the plant ecologist

II Large evolutionary tendencies

A Sterility

Within certain groups of plants what is apparently the natural phylogenetic sequence of genera and species indicates evolutionary progress in the direction of establishing parthenogenesis (The most notable example is provided by the Compositae although it would certainly be unsafe to conclude therefrom that the ultimate goal of plant evolution was parthenogenesis Quite on the contrary one feels that the Compositae have seriously handicapped themselves so far as future possibilities are concerned by a freakish evolutionary maneuver)

C Self sterility

In effect evolution among angiosperms has achieved self sterility through the perfection of devices favoring cross pollination Here should be cited floral adjustments insuring cross pollination by insects protandry and protogeny dioecism

(B Semi sterility

This class has little more than a theoretical existence here although doubtless some forms might be found exhibiting the incompletion of some of the above mentioned evolutionary tendencies and thereby exhibiting what is in effect semi sterility)

III Phenomena of genetics

Here are included cases where the mechanism underlying the phenomenon is affected by breeding operations

A Sterility

1 Wide crosses

Crosses between distantly related parents may be effective in producing first generation hybrids which may be notably vigorous individuals (see chapter on Hybrid vigor) but quite sterile A notable example of this is the cabbage radish hybrid which achieves astounding proportions but is completely sterile (GRAVATT 8)

Here the loss in efficiency in the reproductive system is distinctly not accompanied by loss in efficiency in vegetative development This peculiarity is clarified by the following idea Wide crosses involve the fusion of relatively inharmonious gametes which might be expected to produce disturbances in the ontogeny of the resulting individual The grosser mechanism which regulates vegetative development can evidently weather such disturbances while the more finely balanced mechanism of gamete formation is upset

2 Inbreeding

(This again might be used as an example of opposite extremes of causes producing the same end result for inbreeding can surely be regarded as the antithesis of wide crosses)

Inbreeding commonly results in loss of vigor through the production of weakling and degenerate plants of various types (see chapter on Hybrid vigor) Frequently these degenerate types exhibit faulty and ineffective reproductive parts Types of this sort have frequently been obtained through inbreeding corn

3 Definite hereditary factors

A good example of this appears in the case of tunicate or podded corn Plants homozygous for the tunicate factor are sterile while the heterozygotes are partially sterile (EYSTER 7)

B Semi sterility

1 Wide crosses

The hybrids produced by wide crosses are not in all cases completely sterile (see III A 1) but merely show an abortion of part of the gametes notably part of the pollen This phenomenon is in fact of such general occurrence that the existence of a certain amount of defective pollen is frequently used as a criterion of hybrid origin Many plants in nature have been found to show this characteristic and such plants have been called crypt hybrids the implication being that they are hybrids that have resulted from natural crossing

2 Inbreeding

Some of the degenerate plants that commonly appear as a result of inbreeding (see III A 2) are not completely sterile but merely unsuccessful in setting more than a few seeds This may be due to a failure of part of the pollen or part of the ovules or part of both

3 Definite hereditary factors

Corn which is heterozygous for the tunicate factor (see III A 3) is partly sterile

Here also comes a very unique case which will be described in some detail since it not only provides an ideal example of systematic semi sterility through the operation of definite hereditary factors but at the same time it provides an example of inheritance in the gametophyte generation

BELLING (2) made a cross between two races of bean both of which were completely fertile The resulting hybrids were semi sterile Uniformly just one half of the pollen grains appeared empty and collapsed while one half of the ovules had no embryo sacs The sterile pollen and ovules appeared in random distribution with the fertile

Inbreeding the semi sterile hybrids BELLING obtained an F generation which showed the following features one half of the plants had perfect pollen the other half had a mixture of equal numbers of good and bad pollen grains in all their flowers The plants which had perfect pollen also had perfect ovules while the plants with 50 per cent sterile pollen also had 50 per cent sterile ovules In the F_3 generation all the descendants from the fertile plants had perfectly good pollen and ovules but the progeny of the semi sterile plants again split up into the two classes fertile and semi sterile as before

BELLING states his general conclusion as follows The explanation of the random abortion of one half of the pollen and one half of the embryo sacs must apparently be by the segregation of Mendelian factors among pollen grains and embryo sacs individually and not by the action of these factors on the zygotes

To make this situation clear a diagram (fig 1) may be considered It enlarges a little upon BELLING S original ideas as he stated them and emphasizes the sporophyte gametophyte relationship Pollen grains and embryo sacs are gametophytes in the sense that they include the male and female gametophytes so that when the diagram shows sterile gametophytes it is the same as saying that both pollen grains and embryo sacs are sterile This of course is just what BELLING found whenever one half the pollen grains in random distribution were sterile one half the embryo sacs in random distribution were also sterile

It should be remembered that BELLING started with two completely fertile races Suppose that the parent race *A* had a factor *X* whose absence brought sterility in the gametophytes (pollen grains or embryo sacs) Race *B* had a different factor *Y* with similar effect but inherited independently When BELLING crossed these races all of the resulting F hybrids were semi

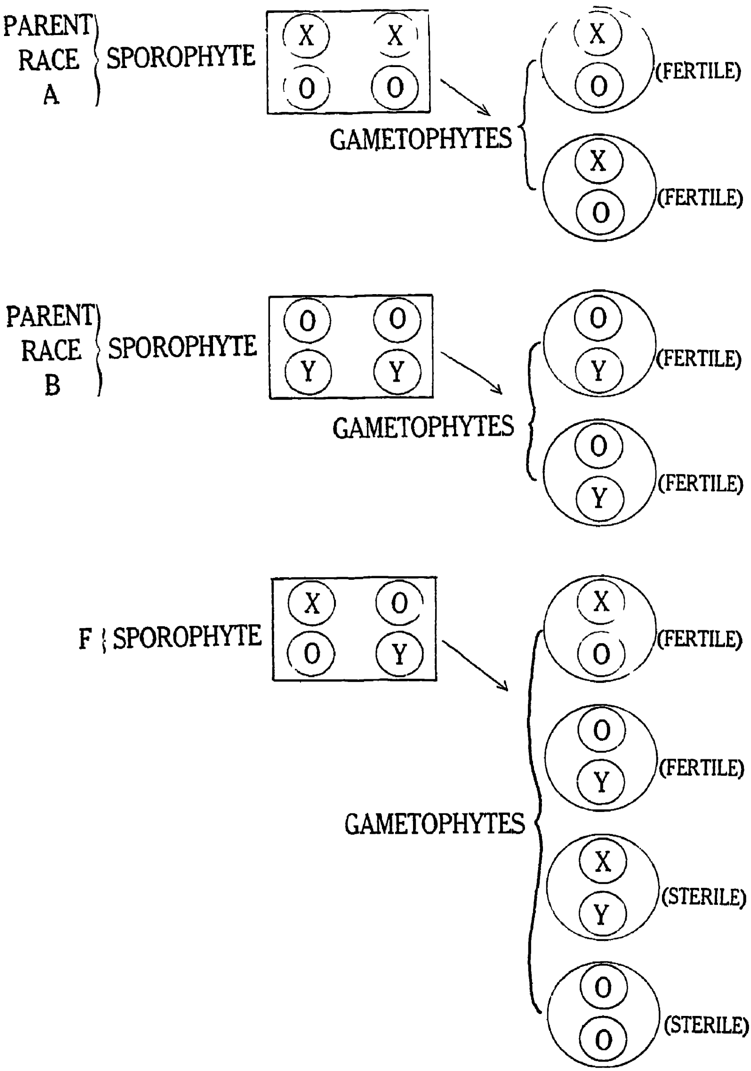


Fig. 21.—Diagram illustrating Belling's explanation of semi-sterility.

sterile In other words in every F plant one half the gametophytes were sterile It is easy to see why XO and OY are fertile also why OO is sterile (lacking both factors) but why should XY be sterile when it has both factors? BELLING explains it by saying that gametophytes are unlike sporophytes in that they normally have single factors instead of double factors The germinal capacity of a gametophyte is just one half that of a sporophyte It is as if a gametophyte were supersaturated by a double factor Such a situation is abnormal for a gametophyte and brings abnormal results Therefore the gametophyte having the abnormal double dose (XY) is just as sterile as the gametophyte with no dose (OO)

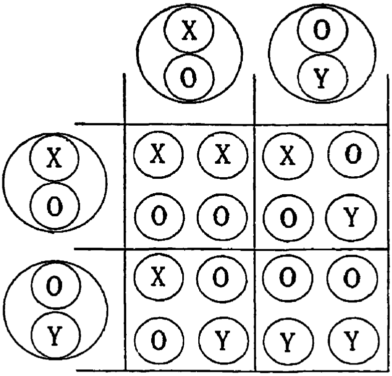
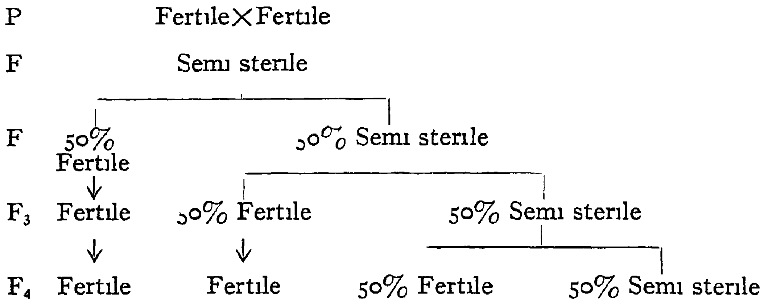


FIG 2 —Diagram showing how the F would be produced according to BELLING s idea of semi sterility

In developing the F ratios of course only the fertile gametophytes function XY and OO are eliminated so far as posterity is concerned so that we have to deal only with the chance matings among the fertile gametes (XO and OY) According to the laws of chance there are four possible matings between these gametes (fig 22) Out of the four resulting F sporophytes two would evidently produce only fertile gametophytes and would remain fertile as long

BELLING s rather awkward assumption to the effect that the gametes with the double dose (XY) are non functional on account of being supersaturated might be improved upon by the following Assume race A has complementary factors X and O for fertility while race B has a similar set of complementary factors Θ and Y located on the corresponding chromosomes The scheme then works out as before gametes of the ΘO and XY formulas both bein non functional for the same reason that a necessary pair of complementary factors is not present as they were inbred The other two are exactly like the original F hybrid and therefore semi sterile having one half sterile gametophytes The whole dynasty may be represented as follows



This is a very ingenious scheme and like most others should be tested by further experiments To a certain extent it has already met this test for BELLING (3) has subsequently reported a few more generations in which the breeding results were entirely consistent with those of the earlier generations Also he has discovered two new races of beans which give similar results

C Self sterility

This is a phenomenon which has loomed up as a great practical problem during the last few years Where pollen and ovules are entirely healthy and functional in out crosses but quite ineffective in bringing about self fertilization the condition of self sterility is said to exist This frequently appears in certain of our important horticultural plants such as apples and plums so that it has often been found necessary to include a mixture of several varieties within the orchard in order to insure effective pollination Many investigators have been attacking this problem with various techniques the most critical work from the point of view of geneticists being that of EAST on *Nicotiana*

By crossing self sterile with self fertile species EAST (6) has demonstrated that self sterility behaves in inheritance like a simple Mendelian recessive to self fertility a single gene evidently determines the difference between the two conditions EAST (4) has further made an attempt to analyze the relations of self terile plants *inter se* In his earlier cultures he had found that the self sterile plants were consistently cross fertile that is there might be quite a group of individuals each one of which would set seed when pollinated from any of the other individuals but would not set seed when self pollinated EAST concluded that when one is dealing with self sterile plants (those lacking the gene for self fertility) pollen is effective only when it comes from a source that has a somewhat different germinal constitution from that of the ovules If therefore a group of self sterile plants is consistently cross fertile it is to be concluded that every individual of this group differs in some degree from every other individual of the group with respect to a certain set of factors that is effective in this connection If this assumption is correct it should be possible in the later generations to obtain groups of individuals all of the same genotype with respect to the effective factor The individuals of any such group should then be cros sterile with reference to each other EAST actually obtained such groups among the later generations thus supporting his assumptions on the relations of self sterile plants *inter se* An exact factorial analysis has not been pos ible as yet but it is plainly a matter of Mendelian inheritance and the general mechanism is rather clearly indicated

Much work remains to be done on the physiology of elf sterility although a few interesting findings have already been made on that matter It has been discovered (at least for a great many cases of self sterility) that the problem is tied up with the growth of the pollen tube Own pollen quite healthy and func tionable on foreign stigmas will also germinate and start pollen tubes on own stigmas Such tubes however are for some reason not successful in reaching the ovules Assumptions were made by various authors that own stigmas poison own pollen tubes or furnish them with inadequate nutrition One author (MOORE 9) has assumed that own stigmas provide own pollen tubes with too good nutrition so that the tubes fatten but do not elongate (just as the hypha of a fungus will elongate more on a poor nutri tive medium than on a good one) EAST (5) himself has done some critical work however that indicates the inaccuracy of all of the foregoing assumptions and reveals an interesting phenomenon that actually accounts for the results in the matter Through careful sections of stigmas made at intervals EAST discovered the following fact Own pollen germinates on own stigmas just as readily as does foreign pollen and the first increment of growth of the two types of tubes takes place at the same rate After that own pollen tubes continue to grow steadily and normally at the same rate at which they started but the rate of growth of foreign pollen tubes is continuously accelerated as though they were receiving some stimulus which was ineffective on own pollen tubes The result is that own pollen tubes fail to reach the ovary before the stigma and style have decayed while foreign pollen tubes with their accelerated growth reach the goal before the road has become blocked

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CHAPTER XI

THE ENDOSPERM IN INHERITANCE

We have dealt chiefly with inheritance in the sporophyte in connection with which most of the work in plant genetics has been done Brief mention has been made of inheritance in the gametophyte on which there has been very little work It is appropriate now to consider inheritance in the endosperm This classification raises the question as to the nature of the endosperm It was at one time generally regarded as belonging to the gametophyte generation but since the discovery of double fertilization in 1898 many have claimed that it belongs to the sporophyte generation On the basis of chromosome numbers it is neither so that there is also the claim that endosperm is neither sporophyte nor gametophyte at least we are justified in considering inheritance in endosperm as a separate topic As might be inferred endosperm shows some features characteristic of a gametophyte others characteristic of a sporophyte and still others peculiar to itself Judgment as to its nature therefore will depend on which of these features is emphasized

It is generally believed that angiosperms have been derived from gymnosperms and it is natural therefore to explain angiosperm structures by the corresponding structures of gymnosperms The gymnosperm and angiosperm ovules are contrasted in fig 23 which will assist in the following discussion In gymnosperms the situa tion is clear After the germination of the megaspore everything within the old megaspore wall is gametophyte

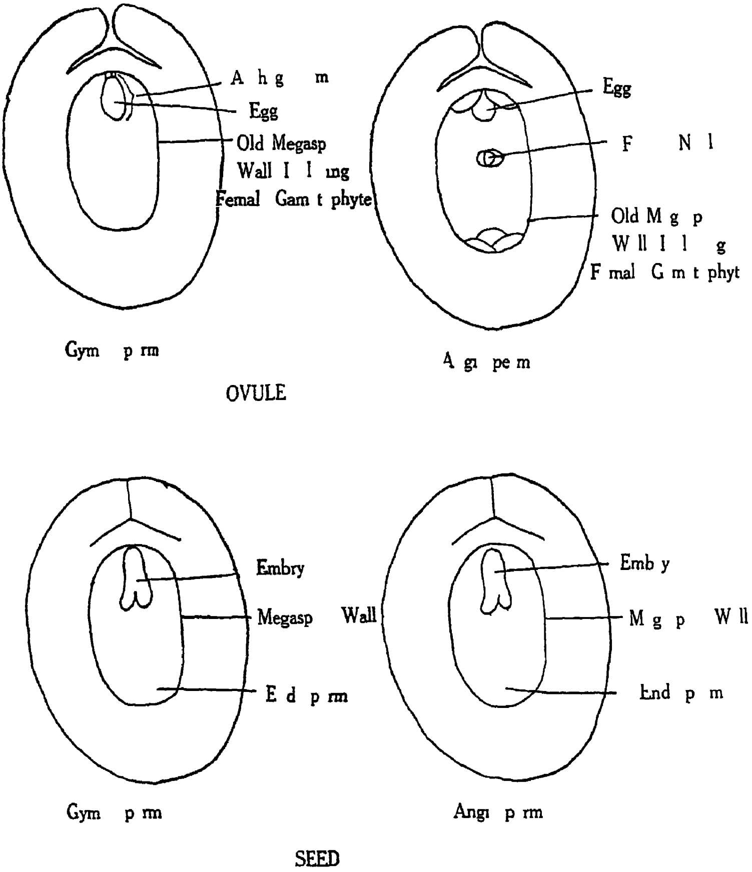

FIG 3 —Diagram contrasting young ovules and mature seeds of ymnosperms and angiosperms

tissue fertilization affects the egg only resulting in a sporophyte embryo In the seed therefore the embryo is imbedded in nutritive tissue which is evidently the vegetative body of the female gametophyte and this tissue is called the endosperm In angiosperms however a new situation introduces doubt It can be said as before that after the germination of the megaspore everything within the megaspore wall is female gametophyte tissue but it cannot be said that fertilization affects the egg only for one of the sperms fuses as regularly with the fusion nucleus as does the other sperm with the egg It will be remembered that the fusion nucleus is formed by two nuclei which have migrated from each end of the sac so that when the sperm enters into the fusion there is a triple fusion After fertilization the fertilized egg of course forms the embryo sporophyte but usually every nucleus of the old gametophyte disappears except the fertilized fusion nucleus which then forms the endosperm in which the young sporophyte is imbedded For this reason the fertilized fusion nucleus is usually called the endosperm nucleus

A comparison of the angiosperm and gymnosperm seeds reveals the following contrast (fig 23) In the appearance of their essential structures they are exactly alike and on that basis some might claim that the endosperm of angiosperms is the same as that of gymnosperms that is gametophyte tissue The opposing claim is that although the gymnosperm endosperm is gametophyte tissue the situation in angiosperms is essentially different In angiosperms the endosperm does not arise from morphologically unmodified gametophyte tissue as in gymnosperms but entirely from the endosperm nucleus and this nucleus is clearly the product of fusion of male and female nuclei With such an origin the endosperm nucleus is comparable with the zygote and the endosperm tissue is sister to the embryo sporophyte In other words in angiosperms the endosperm and embryo are twins This means that the endosperm of angiosperms belongs to the sporophyte generation although of course it is a distinct individual which produces no progeny The embryo sporophyte is a parasite upon its twin and devours it

It will be recognized that there is some reason for both of these claims Is there any way of testing the claims that is of distinguishing between sporophyte and gametophyte tissue? The cytological distinction based on chromosome count is that the sporophyte is $2x$ tissue and the gametophyte is x tissue Applying this test it is found that endosperm tissue is neither x nor $2x$ but $3x$ as might be expected from the triple fusion The conclusion involves several possibilities as follows $3x$ is evidently nearer $2x$ than x and therefore endosperm tissue is more like sporophyte than gametophyte tissue but on the other hand two of the x s have come from the female gametophyte and therefore two thirds of the endosperm is female gametophyte On the basis of predominance therefore endosperm tissue is more like female gametophyte tissue than anything else Finally there is a third alternative and that is that the $3x$ condition deserves to be set apart in a category by itself which would mean that endosperm is neither gametophyte nor sporophyte

These are the claims and the evidence as to the angiosperm endosperm Opinion is not settled but the facts are clear This prepares for a consideration of the bearing of this situation upon genetics The geneticist is not much concerned about the exact morphologi cal or physiological nature of endosperm but he is much concerned about its behavior in inheritance Perhaps the phenomena of endosperm inheritance may help to decide whether endosperm is gametophyte or sporophyte or neither

Certain races of corn have yellow endosperm while in other races it is white (colorless) If a cross is made with pollen from the yellow endosperm race on the silks of the white endosperm race what results would be expected? We could assume that yellow is dominant over white since yellow is probably due to the presence of a factor which is absent in white In making such a cross therefore we should expect a hybrid embryo to be formed which would show the dominant character of yellow endosperm when this embryo becomes a plant bearing ears the next season On the contrary we find the dominant yellow character appears the same year that the cross is made The cross of course puts the yellow endosperm factor in the young hybrid embryo but we cannot imagine that this embryo passed the character out into the endosperm that surrounds it The real mechanism is as follows

Some time after this phenomenon was discovered in 1872 it was named xenia (in 1881) the definition of the term being the direct effect of foreign pollen upon the endosperm At the time of its discovery the mechanism involved in xenia was not understood Later double fertilization was discovered and this furnished the necessary mechanism A pollen grain from the yellow endosperm race contains two male gametes and each gamete contains the factor for yellow endosperm One of the gametes fertilizes the egg and produces a hybrid embryo which in the next generation behaves as a heterozygote for yellow endosperm The other male gamete fertilizes the fusion nucleus and produces the endosperm nucleus which therefore contains the factor for yellow the result being that the endosperm is yellow although the ovule belongs to the white race Xenia means therefore that the endosperm is a hybrid as well as the embryo and the triple fusion involves the transmission of hereditary characters Fertilization of the fusion nucleus is just as essential as fertilization of the egg and so far as inheritance is concerned the endosperm and embryo are sister sporophytes

The exact function of double fertilization is not clearly understood NEMEC (7) has sought to account for endosperm hybridization as an adaptation which results in a better adjustment of the composition of the reserve food supply to the needs of a hybrid embryo

Xenia throws considerable light on the nature of endosperm Because of its behavior in inheritance geneticists would naturally regard the endosperm as a sporophyte an abnormal sister to the embryo

The phenomenon of xenia is not limited to the case of yellow endosperm but appears in connection with quite a number of endosperm characters The red grain and purple grain characters in corn which were employed to illustrate types of factor interaction are also governed by this mechanism In these cases however an additional detail appears A section of a grain of corn appears in fig 24 There is first the pericarp or seed coat which is the ovary wall belonging to the old sporophyte and therefore does not concern us Within this is a thin aleurone layer which is the outer layer of endosperm while the bulk of the seed consists of the starchy endosperm Since aleurone is endosperm colors peculiar to it would show xenia in inheritance This was the case in EAST s red and purple corn the colors being located in the aleurone layer

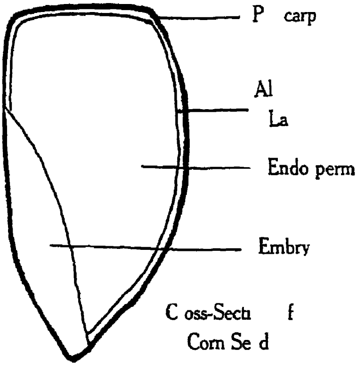

FIG 4 —Diagram of corn seed

There is another phase of the situation to which attention should be called By pollinating the silks of a white grained individual with pollen from a red grained individual xenia is secured the resulting grains being red like those of the pollen parent In the reciprocal cross however that is pollinating silks of a red grained individual with pollen from a white grained individual a different result is obtained The resulting grains are not white like those of the pollen parent but red like those of the ovule parent There is no xenia therefore for the pollen has no immediate effect upon the developing endosperm This seeming difficulty however is easily explained When the pollen parent is white and the ovule parent is red the endosperm gets its characters from both parents and since red is dominant over white the resulting endosperm will be red because the female nuclei that entered into the triple fusion carried the factor for red endosperm and therefore the pollen from the white parent seemed to have no effect The mechanism works in all cases but owing to dominance xenia appears only in certain cases There is no need to dis cuss all of the Mendelian situations in which xenia may occur An understanding of the underlying mechanism should enable us to analyze such cases and reach a conclusion as to the expected results

A law which East (1) has formulated in reference to xenia is pertinent ‘ When two races differ in a single visible endosperm character in which dominance is complete xenia occurs only when the dominant parent is male (pollen parent) When the two races differ in a single endosperm character in which dominance is incomplete or when they differ in two characters (factors) both of which are necessary for the development of the visible difference in both of these cases xenia occurs when either parent is male This may be called the law of normal xenia What may be called abnormal xenia should now be considered

In connection with some of his work on sweet and starchy corn East (1) was able to distinguish two distinct races of starchy corn In one race the starch occurred in a loose powdery or floury condition while in the other race it was compacted into a hard flinty or so called corneous condition The two races therefore may be spoken of as floury and corneous races of starchy corn

East made various crosses between these two races to discover the method of inheritance of the two endosperm characters Naturally such characters would be expected to show xenia In the following description therefore when the F generation is referred to both the hybrid embryo and the hybrid endosperm surrounding it will be included

When East used the floury race as the pollen parent and the corneous race as the ovule parent the F genera tion was all corneous When he made the reciprocal cross (corneous pollen and floury ovule) the F generation was all floury This result certainly suggests maternal inheritance for in both cases it is the character of the ovule parent that is transmitted If it is assumed that this is a case of maternal inheritance two problems are encountered (1) to prove that this behavior is not due merely to parthenogenesis (2) to discover the mechanism to explain maternal inheritance in this case

In the first place EAST established the fact that there was no possibility of parthenogenesis Continuing his investigation he inbred the F generation in each case and examined the F progeny If he were dealing with a case of maternal inheritance what should the F generation show? It should be exactly the same as the F generation for in true maternal inheritance a race will go on forever breeding true to the maternal character whether it is self pollinated or cross pollinated If this had been a case of true maternal inheritance EAST should have obtained the following results

Floury × Corneous
(ovule parent) ↓
F Floury
↓
F Floury
↓
etc

Corneous × Floury
(ovule parent) ↓
Corneous
↓
Corneous
↓
etc

Actually however he obtained the following results

Floury × Corneous
(ovule parent) ↓
F Floury
F ½ Floury ½ Corneous

Corneous × Floury
(ovule parent) ↓
Corneous
½ Corneous ½ Floury

The conclusion is that this is not a true case of maternal inheritance EAST offers a very reasonable explanation of these results based upon the peculiarities of double fertilization These characters appear superficially to be maternal for the following reasons The endosperm nuclei are $3x$ $2x$ from the female and x from the male In the characters under discussion the presence of two factors always dominates the presence of one factor thus corneous female crossed with floury male produces progeny that are all phenotypically corneous while floury female crossed with corneous male for the same reason produces progeny which are all phenotypically floury The mother always determines the character of the hybrid endosperm because there are always two female nuclei to predominate over the single male nucleus In the embryo however this predominance does not occur for there only a single female nucleus has fused with the single male nucleus When this hybrid embryo matures therefore it is evident that it will produce gametes of two sorts 50 per cent corneous and 50 per cent floury Since the female is really the only decisive factor so far as endosperm is concerned the ratios appearing among the female gametes in the F generation will be the ratios that will appear also in the F endosperms In other words 50 per cent of the F endosperms will be corneous and 50 per cent floury no matter what may be the source of the pollen It is obvious that the explanation of this peculiar form of apparently maternal inheritance depends entirely upon a clear conception of the phenomenon of triple fusion Conversely this type of inheritance indicates that the triple fusion instead of being merely a meaningless cytological peculiarity is really significant in inheritance

The foregoing case which is the only endosperm character that is inherited in this peculiar way provides a conspicuous criticism of the presence and absence hypothesis (see also pp 51 112) Whichever of the two characters be assumed to be due to the presence of a gene a demonstration is provided to the effect that two absences will dominate one presence In spite of this outstanding exception the terminology of the presence and absence hypothesis is retained by practically all geneticists and is in fact employed even in connection with the case of corneous and floury endosperm

WEBBER (8) in 1900 experimenting on xenia in corn uncovered some interesting anomalies Pollen from a red grained race applied to silks of a white grained race should result in solid red grains if xenia is normal Of course WEBBER actually obtained this result in the vast majority of cases but occasionally there appeared two other types of grains (*a*) white grains covered with numerous irregular patches of red commonly called mottled (*b*) grains of which a large and uninterrupted area of the aleurone was pure white while the remaining area of the aleurone was just as pure red commonly called mosaic For these cases he constructed an ingenious explanation

Normally the second male nucleus fuses with the fusion nucleus and the result is a solid red grain In some cases however the second male nucleus (1) does not join with the other two while in still other cases the second male nucleus (2) fuses with but one of the polar nuclei leaving the other polar nucleus to act independently Either of these irregularities WEBBER felt would serve to account for the anomalous grains for in either case female nuclei would be left to act independently in the formation of part of the endosperm That part of the endosperm would necessarily show colorless aleurone since the female parent to the cross could contribute no color The remainder of the endosperm produced by the male nucleus (either (1) independently or (2) in conjunction with one of the polars) would of course show the red aleurone characteristic of the male parent

The arrangement of the red and white areas sometimes according to the mottling plan and sometimes according to the mosaic might be explained by the usual method of endosperm formation Endosperm formation begins with free nuclear division the resulting nuclei being free in the cytoplasm of the embryo sac The cell walls are not formed for some time sometimes not until nuclear division is completed Before a large number of free nuclei have appeared they move from the central region of the sac and usually become placed near the wall where free nuclear division continues When walls begin to appear separating the nuclei wall formation begins at the periphery of the sac and extends toward the center in what is called centripetal growth This program which is common in seed plants and is known to occur in wheat is doubtless the program in corn If then the second male nucleus fails to unite with the fusion nucleus and each divides separately when their progeny nuclei move out to the periphery of the sac the nuclei of male and female origin may well become more or less mixed In their further division there would be groups of cells of male origin interspersed among groups of female origin The result would be red and white areas on the mature grain intermingled as irregular blotches giving the mottled effect (*a*) On the other hand if the daughter nuclei of the male and female components migrated *en bloc* to the wall of the embryo sac and no mixing occurred between nuclei of the two types the result would be the production of anomalous grains of the mosaic type (*b*)

These ingenious proposals of Webber s helped to focus the attention of other investigators upon the problem imposed by the occurrence of anomalous grains of these two types

Webber s conception of the mottled grains (*a*) was shown to be fallacious by the experiments of Kempton (6) and of Emerson (4) It was found that mottled grains instead of being anomalies as Webber had believed would appear in considerable numbers and with dependable regularity under the proper con ditions The required conditions were peculiar and interesting If the *R* factor enters the cross with the male parent only a mottled aleurone results if the *R* factor enters with the female parent only or with both parents solid red is the result Thus there is a phenotypic distinction between grains having but one dose of the *R* factor (male parent only) and those having two (female parent only) or three doses (both parents) Furthermore this phenomenon will not appear in all races of corn but only in those which contain a dominant factor for mottling (*S* for spotted aleurone as KEMPTON calls it)

WEBBER's explanations (1) and (2) however might still apply to the anomalous grains of the mosaic type (*b*) Proposition (1) that the second male nucleus fails to fuse and acts independently in endosperm formation was proved to be impossible by some of the experiments of EAST (2) Factors *R* and *C* must be present simultaneously for the production of red aleurone A cross between two colorless types *CCrr* and *ccRR* therefore should produce only red grains Even here however aberrant grains sometimes appear part of the grain being red and the rest colorless Failure of the second male nucleus to fuse with the female polar nucleus in such a case would result in a grain which was entirely colorless a thing which never occurred It is only by fusion of male and female nuclei that any part of the aleurone can be red The experiments on this point were sufficiently extensive to demonstrate that the second male nucleus never fails to affect a fusion with at least one of the female nuclei

There yet remained however WEBBER's possibility (2) fusion of the second male nucleus with only one of the female polars the other female polar acting independently This last possibility was disproved by EMERSON (3) in the following interesting manner A colorless sugary type *CCrrsusu* was used as female parent in a cross with a colorless starchy type *ccRRSuSu* The resulting grains were red starchy save for a few aberrant grains which were red in part and colorless in part but starchy throughout WEBBER's proposition (2) fails here since fusion of the second male nucleus with only one of the polars would produce grains which were red starchy in part (from male nucleus fused with one polar) and colorless sugary in part (from independent polar)

These critical experiments served to disprove WEBBER S propositions and proved that the normal program of double fertilization is invariable in corn The occurrence of the occasional anomalous mosaic grains however remained to be explained Somatic mutation was invoked by some as an explanation but proved unsatisfactory for a number of reasons

EMERSON (5) has finally obtained critical evidence which indicates a very satisfactory explanation of the phenomenon The factor *wx* for waxy endosperm (*Wx* corneous endosperm) is known to be carried on the same chromosome with the *C* factor A cross was made between a colorless waxy female parent *c wx c wx* and a red corneous male parent *C Wx C Wx* (the *R* factor being present in both parents) The resulting triploid endosperm was of the formula *c wx c wx C Wx* If non disjunction (passing of both halves of a divided chromosome to one pole) occurred in connection with the third of these chromsomes one of the resulting nuclei would be diploid for this chromosome set *c wx c wx* and the other tetraploid *c wx c wx C Wx C Wx* Endosperm produced by the former should be colorless waxy endosperm produced by the latter should be red corneous EMERSON obtained aberrant grains which were of exactly this constitution the colorless areas being at the same time waxy and the red areas corneous This experiment considered together with the previous ones indicates that occasional non disjunction is the explanation of these aberrant grains

(The frequency of these particular aberrant grains is one in 423 and one may expect non disjunction to take place in connection with some one chromosome in the corn endosperm in about one of every fourteen grains Direct cytological demonstration is to be hoped for Non disjunction is known to occur at times elsewhere in the plant and animal kingdoms Possibly the triploid nature of endosperm furnishes an especially favorable condition for its occurrence)

This fascinating series of experiments shows how features of the morphological and cytological program in a plant may be demonstrated in a very convincing way through the indirect evi dence provided by careful breeding experiments where it would be rather hopeless to effect any such convincing demonstration through direct morphological or cytological examination

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CHAPTER XII

HYBRID VIGOR

The phenomenon of hybrid vigor has already been referred to It is a matter so intimately related to genetics particularly plant genetics both on the theoretical side and in connection with practical breeding that it will be worth while to consider it in some detail here

The first record of observations on hybrid vigor is that of KOLREUTER in 1776 who states that crossing results in an increase of general vegetative luxuriance and in an increase in the facility of vegetative propagation and viability Later GARTNER discussed the same phenomenon but gave no important new ideas Finally hybrid vigor attracted the attention of DARWIN (4) who states that crossing hastens the time of flowering and maturing and increases the size of the individual He adds the very important fact that it is not mere crossing that gives the stimulus but crossing forms that differ in the constitution of their sex elements in other words crossing between different flowers on the same plant gives no advantage nor does crossing two individuals which are germinally identical He assumed (incorrectly see p 161) that any effective germinal difference was to be accounted for by the fact that the parents had been growing under different environmental conditions

It is probably DARWIN who is responsible for bringing hybrid vigor to the attention of botanist although the modern popular impression might be that BURBANK deserves the credit because of his experience in producing some remarkably fast growing large and vigorous hybrids

Even Mendel s classic pea hybrids supplied further instances of increase in size resulting from crossing Stems of 1 foot and 6 feet in length yielded without exception hybrids which varied in length between 6 feet and 7½ feet (see East and Jones 6)

Among the modern investigators of hybrid vigor Shull East and Jones have contributed much toward an explanation of the phenomenon

Shull s (12) conclusions up to the year 1910 may be summarized as follows His work was entirely with corn and the conclusions contained some very significant points

1 The progeny of every self fertilized corn plant is of inferior size vigor and productiveness as com pared with the progeny of a normally cross bred plant derived from the same source In general this con clusion would be admitted by everyone but it raised one question It was known that when two races have been inbred for many generations they frequently run out gradually losing their vigor In such a case a cross between the two races tends to restore the original vigor The remaining question however is whether the same result may be effected by a cross between two inbred races which have not run out but remain in normal vigor Shull answers that hybrid vigor is exhibited when both parents are above the average condition as well as when they are below it

2 Another question which naturally arises is as follows When these crosses are made it is of course the F generation that shows the hybrid vigor It the F generation is inbred what is the status of the F and later generations with reference to vigor? Shull

answers this question in the following general way The decrease in size and vigor which accompanies self fertilization is greatest in the first generation and becomes less and less in each succeeding generation until a condition is reached in which there is (presumably) no more loss of vigor ’ The facts involved in this statement may be represented in fig 25 In this figure it can be seen clearly that the great loss of vigor comes immediately after self fertilization again begins After that self fertilization brings additional loss in vigor but this loss is less with each succeeding generation It is as though a very definite limit were being approached and each generation goes down one half of the remaining distance toward that limit Just why and in what way this limit is approached will be considered later in connection with the work of EAST and JONES

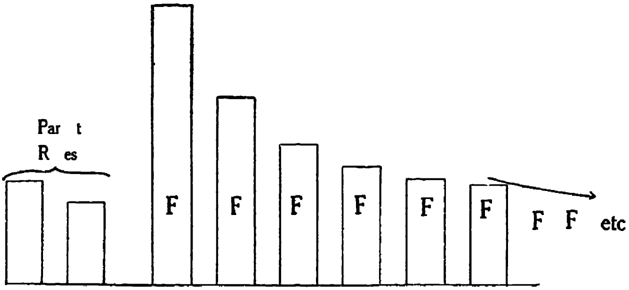

FIG 25 —Illustrating status of hybrid vigor in F and later generations Vigor represented by height of rectangles

3 A cross between sibs (sister and brother) within a self fertilized family shows little or no improvement over self fertilization in the same family This it will be noticed is simply carrying a little further the point that DARWIN originally discovered We realize

that an inbred race should be homozygous therefore all the individuals involved would have the same germinal constitution A cross between any two such individuals would really not be effective in producing a hybrid so that it would not be surprising that such a cross fails to bring hybrid vigor

4 A cross between plants belonging to two self fertilized families results in a progeny of as great vigor size and productiveness as are possessed by families that have never been self fertilized The conclusion from this is that inbreeding results in no permanent loss of vigor A race may ‘ run out if inbred continuously but when crossed with another race it immediately seems to regain all the original vigor It is as though all germ plasm contains the potentiality of developing vigorous individuals This potentiality however cannot express itself until the proper combination of conditions arises and this proper combination seems to be connected in some way with hybridizing

5 Reciprocal crosses between two distinct self fertilized families are equal in producing hybrid vigor When reciprocal crosses are equal it suggests a Mendelian phenomenon Is it possible that hybrid vigor may be explained in terms of Mendelism ?

These are five ‘ laws of hybrid vigor presented by SHULL in 1910 It should be noted that they are not hypotheses but observed facts The hypotheses were developed later when more of the facts were in

A practical suggestion made by SHULL in connection with hybrid vigor is of interest Granted that hybrid vigor is an established fact the question of its practical use in connection with crop plants should be taken into account If a farmer after years of work has finally developed a desirable new strain of corn by selection he is not likely to favor hybridizing with some other strain in any wholesale way He must preserve his pure strain at all costs SHULL has suggested the following solution of this practical problem as indicated in fig 26 Two desirable strains (*A* and *B*) are developed One small plot (I) is planted entirely with *A* and at some distance another small plot (II) is planted with *A* and *B* in alternating rows Plot I is used only to perpetuate *A* in pure condition In plot II all the *A* plants are detasseled The silks of these *A* plants therefore are pollinated by *B* pollen only and the resulting grains in the *A* rows are all bound to be hybrids Using these grains as seed for the crop hybrid vigor will be obtained At the same time both *A* and *B* are perpetuated in the pure condition since the *B* rows in plot II are always self pollinated as there is no other pollen in that neighborhood This is a very simple solution of the problem without necessitating laborious hand pollination

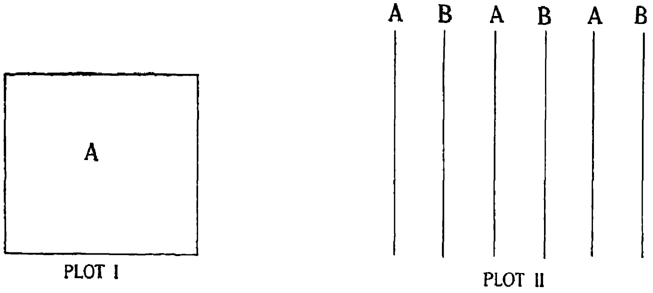

FIG 26—SHULL s scheme of planting for making practical use of hybrid vigor in corn

The investigations and conclusions of EAST (5) may next be considered SHULL did his work entirely with corn but EAST investigated the problem in a more wholesale way After assembling an extensive collection of data he made the summarizing statement that 59 out of 85 angiosperm crosses showed a noticeable increase in vigor East of course did not continue to investigate all of these 85 types but concentrated upon two representatives Corn was selected as representing species normally cross fertilized in nature while tobacco was used to represent those species generally self fertilized in nature

East s results with corn need not be discussed in detail for they confirmed Shull s results in every point It was found that crosses between plants of approximately the same genotype resulted in little or no hybrid vigor even in cases where the two parents to the cross had been grown under different environmental conditions (thus correcting Darwin s misconception see p 156) It was also observed that some crosses resulted in relatively less hybrid vigor than others From such results East developed a very significant and useful Mendelian interpretation of hybrid vigor His proposition is that hybrid vigor is proportional to the number of factors in which the parents differ This situation may be visualized from the following diagram

P t F

$AABBCCDD \times AABBCCdd = AABBCC\underline{Dd}$ = little hybrid vigor

$AABBCCDD \times AABBccdd = AABB\underline{CcDd}$ = more hybrid vigor

$AABBCCDD \times AAbbccdd = AA\underline{BbCcDd}$ = still more hybrid vigor

$AABBCCDD \times aabbccdd = \underline{AaBbCcDd}$ = most hybrid vigor

It is the F of course that shows the vigor but what index can be obtained from the germinal formula of the F generation as to the amount of hybrid vigor that it will show? It is evident that this index lies in the fact that hybrid vigor is proportional to the number of factors that are in the heterozygous condition in the F generation Thus in the first case shown in the diagram there is only a single heterozygous set (*Dd*) and the result is little hybrid vigor Following down the diagram it will be noted that 2 3 and 4 of these heterozygous sets bring an increasing amount of hybrid vigor These are the facts that lie at the basis of EAST s theory which he calls *heterozygosis* This term should not be confused with *heterosis* which is commonly used to express merely the fact of hybrid vigor

We shall now consider how this conception of heterozygosis serves to account for the phenomena that SHULL had previously discovered in connection with hybrid vigor

1 The fact of hybrid vigor —Heterozygosis suggests that hybrids are vigorous on account of the heterozygous sets of factors that they contain

2 The decrease in vigor after self fertilization begins again —The greatest loss in vigor comes between the F and F generations Thereafter the loss becomes gradually less each generation approaching a definite limit beyond which no further loss in vigor occurs Heterozygosis explains this as follows

$$AABBCCDD \times aabbccdd = AaBbCcDd$$

In this case the F generation is 100 per cent heterozygous all four factor sets being heterozygous and therefore it is very vigorous In later generations as is well known more or less homozygous sets will be split off Introducing homozygous sets into some individuals will reduce the aggregate heterozygous condition of the whole population to something less than 100 per cent there will therefore be a corresponding loss in vigor

If the genotype of the F population be considered (a simpler example *AABB*×*aabb* will suffice) some very clear conclusions may be drawn The F population is heterogeneous with respect to hybrid vigor in sharp contrast with the F where all the individuals showed the same amount of hybrid vigor In the F there will be one genotype which is heterozygous with respect to all of the factor pairs involved (as was the F) and which therefore shows the maximum amount of vigor There will be other genotypes which are homozygous with respect to all the factor pairs and show no vigor And there will be still other genotypes which are partly heterozygous and partly homozygous and show an intermediate amount of vigor This heterogeneity of the F generation with respect to amount of hybrid vigor is in agreement with the actual experimental results

If the average vigor of the whole F population be computed in terms of relative numbers of factor sets in the heterozygous condition this will be found to have a value of 50 per cent in contrast with the 0 per cent of the original grandparental generation and the 100 per cent of the F On the same basis the F_3 will be found to have 25 per cent the F_4 12 5 per cent and so on exactly one half of the vigor being lost with each succeeding generation of inbreeding This serves to account for SHULL s observation that the greatest loss in vigor is between the F and F generations Thereafter the loss gradually approaches the limit when the perfectly homozygous condition is reached for the whole population and then there can be no more loss in vigor

3 A cross between sister and brother effects nothing —This is evident for it introduces no heterozygosity

4 A cross between plants belonging to two self fertilized families results in a progeny of as great vigor size and productiveness as are possessed by families that have never been self fertilized —Heterozygosis accounts for this by showing that a cross between two

pure lines may bring into the hybrid a maximum number of heterozygous sets quite as many as are present in cross fertilized families

5 Reciprocal crosses are equivalent —This would obviously follow from any Mendelian hypothesis such as heterozygosis

EAST next studied tobacco as representing those species which are generally self fertilized in nature It is a common impression that tobacco is a striking exception in the matter of hybrid vigor In tobacco crosses the hybrid progeny instead of being more vigorous are frequently less vigorous than either parent EAST admits that there are certain cases of this kind but points out a number of other cases which are quite normal in showing hybrid vigor In any event the tobacco situation strongly suggests the idea that hybrid vigor appears less prominently in species that are generally self fertilized in nature than in species normally cross fertilized

It may be that the subnormal tobacco hybrids are products of such wide crosses that hybrid vigor can no longer operate (see p 169)

The phenomenon of hybrid vigor appears also in a great many other plants It has of course been noted most frequently in cultivated forms but there is also some evidence as to its occurrence among wild plants Not only has it been observed among many angiosperms woody as well as herbaceous but also among gymnosperms and pteridophytes and there is even some slight evidence that hybrid vigor occurs in the sporophyte of the bryophytes (see BRITTON 1)

As for the exact nature of the phenomenon quite a number of features are involved Primarily hybrid vigor amounts to an increase in the size of cells as well as multiplication in the number of cells in other words an increase in the power of assimilation Viability of seeds is increased and the more rapid growth and earlier maturity of the seedlings is quite noticeable Time of flowering and maturing is hastened although in many cases increased longevity has been brought about One sees a distinct increase in the size of the roots In the stem there is no increase in the number of nodes but the internodal development is striking (The gain in size in plants which are more or less determinate in their number of parts is made up of an increase in the size of parts rather than in the number of parts) Usually the stem growth is greater than the leaf growth but the increase of the latter can be definitely traced The size of the flower is usually not affected nor is there any change in the size of small fruits such as tobacco In fleshy fruits however such as tomato and egg plant there is a marked increase On the individual plant there are distinctly more flowers and fruits and in some cases separate inflorescences are longer as in the ears of corn (Total yield in corn has in some crosses been increased 100 per cent or more) Endurance against unfavorable environmental factors and resistance to disease have also been frequently noted as properties of hybrids Facility of vegetative propagation is increased (Moreover there is no evidence to prove that plants lose any of their hybrid vigor in long continued vegetative multiplication through innumerable generations)

In general there is similarity between hybrid vigor and the effect of a good environment Those characters which are the quickest to be modified by external factors also show the greatest change on crossing There is at least one difference between the two however in time of maturity environment and hybrid vigor have somewhat opposite effects Generally speaking favorable growing conditions tend to delay flowering and maturing while conditions which tend to stunt the plants tend like hybrid vigor to hasten them (East and Jones 6)

There seems little doubt that hybrid vigor is also manifested in the animal kingdom One might reasonably expect this from the fact that the principles of inheritance are fundamentally the same in plant and animal kingdoms and hybrid vigor is a matter of inheritance As a matter of fact there are many cases among the records of professional animal breeders which might be cited as evidence of hybrid vigor It seems equally evident however that this is not so general a phenomenon among animals as among plants and it should be noted that many zoologists refuse to recognize in hybrid vigor anything like a general law pointing out cases among animals in which hybridizing apparently results in loss of vigor

It is rather to be expected that such a general phenomenon as hybrid vigor must have played a part in the evolution of the plant kingdom A few suggestions follow (from East and Jones 6)

1 Fixation of characters favoring cross fertilization — Variations must have appeared that favored cross fertilization Those plants producing a cross fertilized progeny would have had more vigor than their self fertilized relatives The crossing mechanism could then have become homozygous and fixed while the advantage due to cross fertilization continued

2 Fixation of sex act itself — Some means of favoring union of dissimilar spores occurred as a chance variation Through the combination of somewhat different qualities this new dual product the zygote was better enabled to develop and reproduce Its survival coefficient was high The tendency for union of spores persisted and became characteristic of the species

3 Preservation of undesirable characters in cross fertilized species — In self fertilized species new characters that weakened

the individual would have been immediately eliminated Only strains that stood by themselves that survived on their own merits would have been retained On the other hand weak genotypes in cross fertilized species were retained through the vigor that they exhibited when crossed with other genotypes The result is therefore that self fertilized strains that have survived competition are inherently stronger than cross fertilized strains On this account weak genotypes may often be isolated from a cross fertilized species that as a whole is strong and hardy

4 Rise of the sporophyte generation —The commonly accepted interpretation of hybrid vigor is based upon a Mendelian mechanism that would be effective only in the diploid generation In the evolution of the plant kingdom the haploid gametophyte generation has been superseded in dominance by the diploid sporophyte generation Hybrid vigor may help to account for this

Some recent investigations have extended the scope of hybrid vigor in an interesting and significant way The work was done originally by COLLINS and KEMPTON (3) and later confirmed and extended by JONES (8) In brief it is as follows

If corn sporophytes exhibit hybrid vigor will the endosperm also show the same phenomenon ? Endosperms as has been stated are genetically equivalent to sporophytes in several ways If crossing increases vigor and size of sporophytes therefore it might be expected to increase the size of the endosperms also

Furthermore the endosperms have considerable advantage over sporophytes as material for such investigation We say that hybrid sporophytes are more vigorous than pure bred sporophytes but just how much more vigorous cannot be stated with exactness In order to demonstrate this clearly it would be necessary to have the hybrid and the pure bred stock growing side by side in exactly the same conditions but the conditions cannot be controlled with exactness The environmental factors affecting the size and vigor of a corn plant are numerous complex and to a large extent uncontrollable Thus two different plants growing side by side might be in a distinctly different environment without the fact being recognized It cannot therefore be said with much certainty just how much hybrid vigor a given plant shows when there are so many unknown factors that might affect size and vigor On the other hand if it is claimed that the endosperm of one grain shows a given amount of hybrid vigor as compared with the grain that grows next to it upon the same ear the statement would be more exact for the two endosperms have developed under conditions which are unquestionably much more constant than the conditions surrounding the different sporophytes in a corn field

JONES selected a plant with white endosperm and pollinated it with a mixture of its own pollen and pollen from a yellow endosperm race In the resulting ear therefore he had a mixture of yellow endosperm grains and white endosperm grains The former grains of course were hybrid since the yellow factor was introduced by the foreign pollen while the white endosperm grains must have resulted from own pollen and were homozygous In this way JONES obtained side by side in the same ear endosperms obviously hybrid and endosperms obviously homozygous When he weighed these two types he found that the hybrids exceeded the homozygotes in weight by from 5 to 35 per cent

He made the reciprocal cross using the same mixture of yellow and white pollen on silks of the yellow race Of course all the resulting endosperms were yellow but the hybrids which had the yellow factor only from the female side were distinctly lighter yellow than the homozygotes which had the yellow factor from both male and female sides Weighing these two types JONES obtained the same results as before the hybrids exceeding the others in weight by an average of 20 per cent This is really the clearest demonstration of hybrid vigor that has ever been provided for the conditions of the experiment were ideally constant

It is interesting to note in this connection that there is no selective action favoring foreign pollen when these pollen mixtures are applied In fact the results indicate that own pollen is successful in bringing about fertilization in a slightly greater number of cases than is foreign pollen

It has been stated that the amount of hybrid vigor varies directly with the width of the cross Of course this statement applies only within certain limits The situation is somewhat clarified by considering the following series of cases which is arranged with respect to width of cross

1 Parents so diverse that cross cannot be made

2 Cross possible but seed obtained fails to germinate Example certain *Nicotiana* crosses

3 Hybrid seed germinates but resulting hybrid plants are so weak that they fail to reach maturity Example other *Nicotiana* crosses

4 Hybrid plants mature and are extremely vigorous but are sterile except possibly in back crosses Example cabbage radish hybrid an enormous but completely sterile plant Example from animal kingdom the mule (On this matter see also chapter on Sterility)

5 Hybrid plants more vigorous than parents and completely fertile Example corn crosses and many others

6 Parents to cross so closely related that no production of hybrid vigor is noticeable

(An interesting phenomenon appears in certain wheat crosse where it is found that the F endosperms are well developed in the fertile crosses but shriveled in those crosses which are to produce sterile or partially sterile F plants Even in these latter cases however hybrid vigor appears in the vegetative parts of the F plants SAX 11)

Obviously it is only within the limits of classes 4 and 5 that it can be said that hybrid vigor varies directly with the width of the cross It is impossible to say where the species boundary fits into the foregoing scheme since species boundaries are more often matters of personal opinion than indices of crossability

The theory of heterozygosis claims that hybrid vigor appears in proportion to the number of factors in which the parents of the cross differ This claim should be considered briefly Is heterozygosis really an explanation of the phenomenon of hybrid vigor? It seems obvious that it is not It was known that hybrids were vigorous because they were hybrids Heterozygosis states that hybrids are vigorous to the degree that their parents differed in hereditary factors in other words this is merely a statement that hybrids are vigorous because they are hybrids with the addition that the more hybrid a hybrid is the more vigorous it is It follows therefore that heterozygosis is not an explanation of hybrid vigor but merely a restatement of the phenomenon in Mendelian terms with the additional idea that there may be various degrees of hybrid vigor It is not the intention to discredit heterozygosis as a valuable conception but to point out that it is not a real explanation merely a more intelligent statement of facts

Furthermore heterozygosis is rather unsatisfactory in another way It locks the door on any hope of originating pure strains having as much vigor as first generation hybrids

For these reasons it would seem desirable to seek an explanation of hybrid vigor along other lines Such an explanation may be developed from the following considerations

In nature a struggle for existence occurs among species and individuals There must occur also a struggle for existence among unit characters If a unit char acter is undesirable it is eliminated for the individual or species that carries it is eliminated This would obviously apply particularly to the dominant characters for undesirable recessives might well survive by escaping natural selection while in heterozygous combination with their dominant allelomorphs It follows that the dominant unit characters that have survived and appear in the plants of today are for the most part desirable ones

The question may be raised as to what constitutes a desirable character It may be any one of a number of things but is there not some feature which is common to all desirable characters? The common feature of all desirable characters would seem to arise from their relation to the vigor of the organism Each desirable character must add somewhat to the vigor of the plant that contains it and associated with vigor are such things as size and productiveness Is it not reasonable that those plants will be most vigorous which have in combination the greatest number of desirable characters? The plants which have the greatest combination of such characters are the hybrids

A diagram similar to that which was used to explain heterozygosis may be considered

$$\overset{P_t}{AABBCCDD \times AABBCCdd} = \overset{F}{AABBCC\underline{Dd}} = \text{little hybrid vigor}$$

$$AABBCCDD \times AAbbccdd = AA\underline{BbCcDd} = \text{still more hybrid vigor}$$

In that explanation it was stated that the first case showed little hybrid vigor because it had only one heterozygous set (Dd) while the other case showed more hybrid vigor because it had three such heterozygous sets Hybrid vigor therefore appeared in proportion to the number of heterozygous sets in the hybrid This diagram served the purpose of explaining heterozygosis but it will now be discarded because it does not represent the most important result when two races are crossed The important result is represented in the following diagram

$$\begin{array}{ll} \quad\text{P}\quad\text{t} & \qquad\text{F} \\ \left.\begin{matrix} AABBCCddeeff \\ aabbccDDEEFF \end{matrix}\right\} & \underline{AaBbCcDdEeFf} = \text{more hybrid vigor} \\ \left.\begin{matrix} AABBccddeeff \\ aabbCCDDeeff \end{matrix}\right\} & \underline{AaBbCcDd}eeff = \text{less hybrid vigor} \end{array}$$

The thought is that in each of these two cases the hybrid is more vigorous than either parent not because it contains more heterozygous sets but because it contains more dominant factors which means more desirable characters For example in the first case each parent contains three factors the small letters representing merely the absence of factors The F generation therefore contains six factors and for this reason is more vigorous than either parent It is stated in the diagram that in the first case there is more hybrid vigor and in the second case less hybrid vigor simply because hybrid vigor is a relative term It represents merely how much more vigorous the hybrid is than either parent In the first case the parents have three factors and the hybrid six the increase being three which measures the amount of hybrid vigor In the second case each parent has two and the hybrid four the increase therefore is only two and for this reason there is less hybrid vigor in the second case than in the first

Assuming that the majority of dominant factors are desirable and that desirable factors make for general vigor it would follow that the most vigorous plant will be the one containing the greatest number of dominant factors It has been shown that the plants containing the greatest number of dominant factors are the hybrids it is for this reason that hybrids are relatively vigorous

The following question may be raised If it is granted that most desirable factors tend somewhat to increase the general vigor do they all do this to the same degree? The natural answer is in the negative but this has no bearing upon the validity of the explanation On the other hand if heterozygosis be accepted for an explanation the question presents a difficulty Heterozygosis would suggest that *Aa* induces vigor not because of any particular factor that it represents but because it is a heterozygous set It seems more reasonable and natural to suppose that certain factors induce more vigor than others

It is evident that the suggestion made above is that of a real explanation of hybrid vigor and not merely a restatement KEEBLE and PELLEW (10) suggested it in 1910 and since that time it has been somewhat discussed in the literature being referred to as the hypothesis of dominance (accounting for hybrid vigor) At first statement the theory seems sound but actually it does not fit the facts The two outstanding objections to this theory of dominance are brought out in the publications of SHULL EMERSON and EAST

1 If hybrid vigor were due to dominance it would be possible in generations subsequent to the F to recombine in one race all of the dominant factors in the homozygous condition Thus there could be isolated a race that was 100 per cent vigorous and since it would be homozygous its vigor would not be lost by inbreeding Actually though no one has (as yet) been able to fix

hybrid vigor in this way ‘ all maize varieties lose vigor when inbred ’

2 Experience assures us that the distribution of individuals in the F generation with reference to hybrid vigor is represented graphically by a symmetrical curve similar to the normal probabilities curve the class containing the greatest number of individuals is that which shows the medium amount of hybrid vigor while on either side of this class the fall in the curve is regular reaching its lowest points in the two small extreme classes which show respectively greatest hybrid vigor and least hybrid vigor According to the dominance hypothesis the largest class of the F individuals is that showing greatest hybrid vigor (if only a few effective factors are assumed as was the case in the work of Keeble and Pellew) while the smallest class would be that showing least hybrid vigor The curve representing such a situation would be asymmetrical and strikingly different from that which actually occurs

For these two reasons the dominance hypothesis as proposed by Keeble and Pellew has been discarded Although it is theoretically attractive its failure to satisfy these two important details of the hybrid vigor situation has condemned it

Recently Jones (7) has ingeniously modified the dominance hypothesis so as to avoid these difficulties The argument is essentially the same with one very significant modification Jones visualizes the situation as represented in fig 27 In this case it is a question of linkage of dominants and recessives The vigor of one parent is due to the two dominant factors *A* and *D* while that of the other parent is due to the two dominant factors *C* and *B* The hybrid is more vigorous than either because it combines all four dominant factors The attractiveness of this scheme lies in the fact that it escapes the objections that were made to the older dominance hypothesis

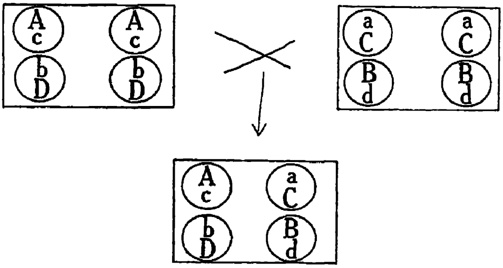

FIG 27 —Diagram to aid in visualizing JONES s explanation of hybrid vigor by dominance of linked factors

1 The fact that 100 per cent hybrid vigor cannot be fixed is quite in accordance with JONES s scheme for it is obviously impossible to isolate a race homozygous for all four factors *A* *B* *C* and *D*

As a matter of fact it would be theoretically possible under this scheme to isolate just such a homozygous race If crossing over took place during gamete formation by the F A and *C* might come to lie on the same chromosome When a gamete containing such a chromosome mated with another gamete of the same sort a race would thereby be established which was homozygous with respect to *A* and *C* If a similar performance took place (either simultaneously or in some subsequent generation) in the other chromosome pair the race would also achieve homozygosity with respect to *B* and *D* and would thereafter breed true for all four factors

It must be evident however that there would be but a remote chance of realizing this theoretical possibility inasmuch as there actually must be many more than two chromosome pairs involved and more than two effective factors on each chromosome At the same time it is rather encouraging to believe that such a possibility exists so that eventually we may be able to obtain a race that is homozygous for all or practically all of the desirable factors

2 A simple mathematical demonstration will show that the distribution of F individuals is quite what it should be represented by a symmetrical curve similar to the curve of probabilities

It can be demonstrated rather rapidly that JONES s scheme will satisfy the requirements on distribution of F individuals with respect to hybrid vigor and on the progressive loss of vigor in the later inbred generations It was seen that the heterozygosis theory could account for these facts by the use of the simple example $AAbb \times aaBB$ As a matter of fact fig 27 becomes the exact mathematical equivalent of this example if we substitute the Ac chromosome of the dominance scheme for A of the heterozygo is scheme the bD chromosome for b the aC chromosome for a and the Bd chromosome for b In this way it will be discovered that the two schemes run exactly parallel in accounting for the facts in every generation

In fact this new theory the dominance of linked factors seems altogether sound and natural We should rather expect that each chromosome would bear several dominant factors conducive to vigor and several recessives as well

Recently COLLINS (2) has presented some interesting considerations bearing on this scheme of JONES s COLLINS maintains that in explaining hybrid vigor one should place the emphasis on the suppression of deleterious recessive characters rather than on the accumulation of dominant growth factors This is merely a change in the point of view COLLINS further maintains however that the dominance scheme can really account for the facts without the assumption of linkage provided a sufficient number of effective factors be assumed There is some rather good evidence to support these contentions of COLLINS For the present how ever JONES S explanation seems distinctly more serviceable than any other that has been offered

SHULL S scheme to take practical advantage of hybrid vigor in such a plant as corn has one distinct drawback As was brought out in chapter ii the size of a corn plant is limited by the size of the seed which produces it and this in turn is limited by the size of the mother plant upon which the seed developed Since SHULL S races *A* and *B* were both inbred races they must have been rather small Consequently whichever way the cross was made the seeds containing the F embryos would be limited in size by the small size of the female parent so that the F plants would get a poor start and would never be able to attain the size that would have been possible had they come from large seeds

JONES (9) suggests a way of overcoming this difficulty Starting with four pure races cross *A* with *B* and *C* with *D* This will result in two vigorous F types either one capable of developing large seeds Cross these two and a double hybrid results which combines in good part the advantages of all four of the original races and is not limited in size by starting from a small seed Of course there is a certain drawback here also since the generation used for the crop is an F with respect to the two original crosses and has somewhat less than the maximum vigor on that account The relative advantages and disadvantages of such breeding plans can be evaluated only by experiment JONES claims to have gotten better results from his double cross method than could be obtained from SHULL S plan

From the discussion that has been presented in this chapter one may safely conclude that the phenomena which arise in connection with inbreeding and outbreeding can be explained satisfactorily in terms of the Mendelian mechanism of inheritance It should be recognized that inbreeding is not injurious per se (through mere fact of consanguinity) but because it serves to isolate undesirable recessive types from a hybrid mixture

The proof on this point is that inbreeding in homozygous stock results in no deterioration JONES (9) has carried on through twelve generations the inbred corn cultures that were started by EAST In the course of this experiment a great number of undesirable recessive types have been thrown off On the other hand certain of the lines that have been isolated by this inbreeding are quite normal and healthy though small in stature and yield A point of homozygosity has been reached where further inbreeding brings no further loss in vigor

On the other hand hybrid vigor does not arise from the act of crossing per se but merely through a combination in the hybrid of the maximum number of desirable factors

On this point the proof lies in the fact that crossing brings hybrid vigor only when the parents to the cross differ in their germinal constitution There is plenty of evidence on this point In JONES s inbreeding experiments a point of homozygosity has been reached where crosses between different individuals of the same line brings absolutely no hybrid vigor

In conclusion attention should be called to the danger of confusing phenomena of hybrid vigor with those of cumulative factors Both mechanisms may operate on some generalized quantitative character such as size but the hereditary behavior is distinctly different Cumulative factors bring an F which is no more variable than either parent type and intermediate in size and later generations which are highly variable The average size of the whole population however is the same for every generation including the parental and the F generations The hybrid vigor mechanism also brings an F no more variable than either parent type (as would any Mendelian mechanism for that matter) and later generations which are widely variable In this case however the average size of the whole population is distinctly different in the different generations In such a matter as size the hybrid vigor manifestations would be superimposed upon the cumulative factor manifestations

It might appear unsatisfactory and arbitrary to assume dominance of factors as essential to explaining hybrid vigor and lack of dominance in the case of cumulative factors It is quite likely however that the fundamental and natural distinction between the two mechanisms lies in this very point Where a number of factors interact in affecting some quantitative character and those factors show lack of dominance a cumulative factor mechanism is thereby set up A similar interaction where the factors are dominant brings into play the hybrid vigor mechanism There is a difference between the two mechanisms simply because some factors show dominance and others do not

This idea may be reinforced by the following theoretical suggestion Where the environment (using the term in its widest sense) imposes no limitation upon the degree to which a character may be expressed it follows that two doses of a factor must have twice the effect of one dominance is lacking Where the environment limits the expression of a character and one dose of a factor results in a development of the character to this limit two doses can affect nothing more dominance is present Furthermore these environmental limitations may shift as the environment changes Such an environmental shift could affect in no way the degree of development of those characters in connection with which there is no dominance but would be expected to affect the degree of development of those characters where dominance occurred According to this idea we should expect non dominance or cumulative factor characters to be of such a sort that the environment never affects the degree of their development while dominance or hybrid vigor characters would be those which environmental changes could also modify For the most part this actually agrees with the facts (see p 165) Further investigation will doubtless provide a more definite answer on this matter

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CHAPTER XIII

SEX DETERMINATION

Sex determination is very properly a part of the subject of genetics It should be realized however that a vast amount of investigation has been carried on in this field and it will be possible here to take up only a limited number of representative cases

Since this subject has been investigated a great deal more thoroughly and for a great many more years in animals than in plants it will be appropriate first to consider some of the findings of the zoologists Until very recently at least there appeared two outstanding and seemingly quite contradictory views as to the basis of sex determination

1 Some believed that sex is predetermined by the chromosome equipment that enters into the zygote

2 Others believed that sex may be determined otherwise than by the chromosomes the decisive factors being certain physiological conditions surrounding the unfertilized egg or the developing embryo

These two general views will be referred to as the chromosome theories and the physiological theories Representative examples of each will be considered briefly

CHROMOSOME THEORIES —A classic example of the simplest kind is to be found in the nematode worms Fig 28 will indicate how sex is determined in this case Both male and female have ten chromosomes (commonly called *autosomes*) to determine most of their somatic characters but in addition there are extra chromosomes that determine sex known as *sex chromosomes* or *heterochromosomes* In this case the male contains only one sex chromosome while the female contains two At the reduction division when the gametes

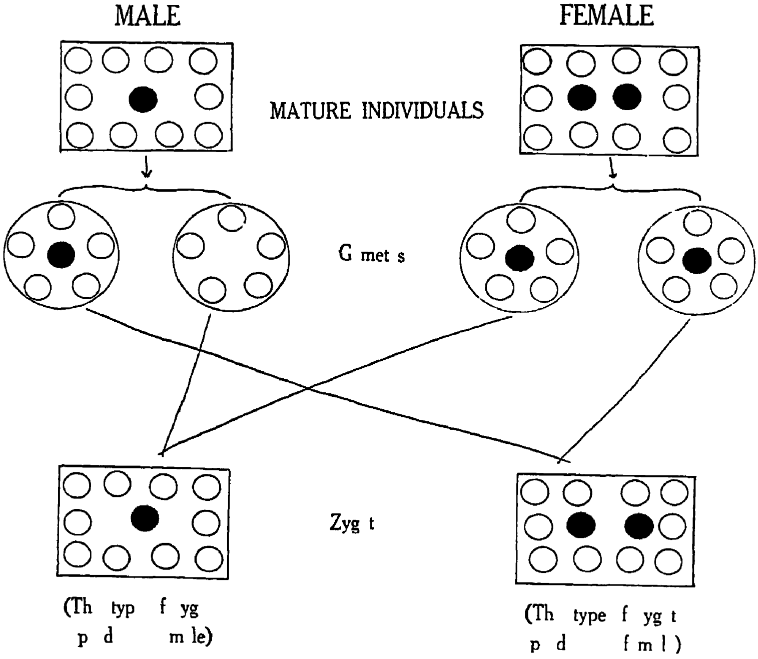
MALE
FEMALE
MATURE INDIVIDUALS
Gametes
Zygotes
(The type of zygote produced male)
(The type of zygote produced female)

FIG 28 —Illustrating behavior of sex chromosomes

are formed the chromosome equipment is reduced one half It is obvious that in the female each egg receives one sex chromosome and therefore all eggs are alike in this feature In the male however with one sex chromosome at the reduction division the solitary sex chromosome goes to one pole leaving the other pole without such a chromosome As a result there are two kinds of sperms one half containing a sex chromosome the other half containing none At fertilization if an egg mates with a sperm having a sex chromosome the zygote contains two and this will develop into a female for females are characterized by two sex chromosomes With a sperm of the other type the zygote receives only one sex chromosome and must produce a male individual As a result males and females are produced in equal numbers sex being determined by the type of sperm that enters into the sex fusion

Certain conclusions may be drawn from this mechanism of sex determination which will serve to provide a sharp contrast with the corresponding conclusions that may be drawn from the physiological theories

a) The sex ratio will regularly be 50 per cent males 50 per cent females It would be rather hopeless to modify this ratio by artificial means

b) Sex is a qualitative matter only two conditions being possible strictly male and strictly female

Numerous instances of the sex chromosome mechanism have been discovered in the animal kingdom Details differ in the different cases but the essential mechanism remains the same In addition to the type of case described above where the male has only one member of the sex chromosome pair there are in general three other possibilities The male may have one large chromosome (similar to the pair in the female) paired with a small one the male may have two sex chromosomes of approximately the same size but different in shape or the male may have two sex chromosomes which are morphologically identical but physiologically different in their influence on sex In all of these cases the fundamental mechanism remains the same the male being heterozygous for sex so that two types of sperms are produced in equal numbers and the sex of the offspring depends upon which type of sperm has effected fertilization In the cases where the male has an unequal pair of sex chromosomes that member of the pair which is similar to the equal pair of the female is known as the X chromosome while the other chromosome of the male is the Y chromosome (XX is female XY is male)

Furthermore although the male is usually the heterozygote for sex there are some cases in which the female is the heterozygote In such cases the sperms are all alike two types of eggs are produced in equal numbers and the sex of the offspring depends upon which type of egg has effected fertilization This is the situation in the birds and in the Lepidoptera group of insects while in practically all of the other known cases it is the male that is the heterozygote for sex

When genes are located on the X chromosome their method of inheritance is characteristic being known as *sex linked* inheritance (This term should not be confused with *sex limited* inheritance which applies to cases where the genes are carried on the autosomes in the usual manner but can express themselves only in one sex e g heavy beardedness in man) Numerous examples of sex linked inheritance are to be found in the fruit fly

The female fruit fly has a pair of X chromosomes while the male has an X mated with a Y the two being distinguishable by their shape Numerous genes are located on the X chromosome but none have been identified on the Y which seems quite negligible in inheritance Vermilion (v) a recessive to normal red eye (V) is a gene of this sort When a vermilion female (vX) (vX) is mated with a red male (VX) Y all of the female progeny are bound to be red (vX) (VX) while all of the male progeny will be vermilion (vX) Y as is explained by fig 29 This has often been called zig zag inheritance since the character of the mother passes to the sons while the character of the father passes to the daughters All of the other possible matings work out just as one would expect from the mechanism that is involved

Some very recent papers (CASTLE 10) have suggested that genes may actually be located on the Y chromosomes in some animals A peculiar one sided type of inheritance results since it is possible for such genes to be present only in the male The author is not as yet certain that these findings will be accepted by other geneticists

In this connection it will be worth while to consider briefly some of the work of **Bridges** (5) which provides the final demonstration that the chromosomes are the bearers of hereditary characters and that the sex chromosomes are really the effective

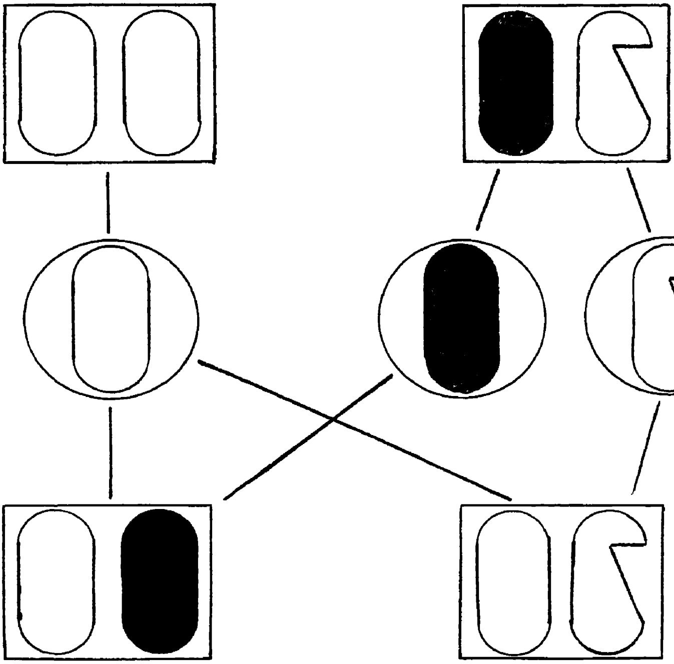

Fig 29—Shaded *X* chromosomes carries gene (*V*) for red eye unshaded *X* chromosome lacks this gene (i e condition) Y chromosome of male distinguished by shape Individuals carrying *V* are red eyed those lacking it are vermilion eyed This diagram shows how vermilion female (upper left) mated with red male (upper right) results in red daughters (lower left) and vermilion sons (lower right)

units in determining sex Occasional non disjunction of the *X* chromosome during gametogenesis in a vermilion female results in the production of two abnormal types of eggs (*v*Y) (*X*) and *O* (fig 30) The matings of these two abnormal types of eggs with the two normal types of sperms from a red male will result in four possible types of zygotes

A (vX) (vX) egg with a (VX) sperm gives a (vX) (vX) (VX) zygote which might be expected to produce a red female but actually dies (according to BRIDGES earlier statements)

A (vX) (vX) egg with a Y sperm gives a (vX) (vX) Y zygote which produces a vermilion female

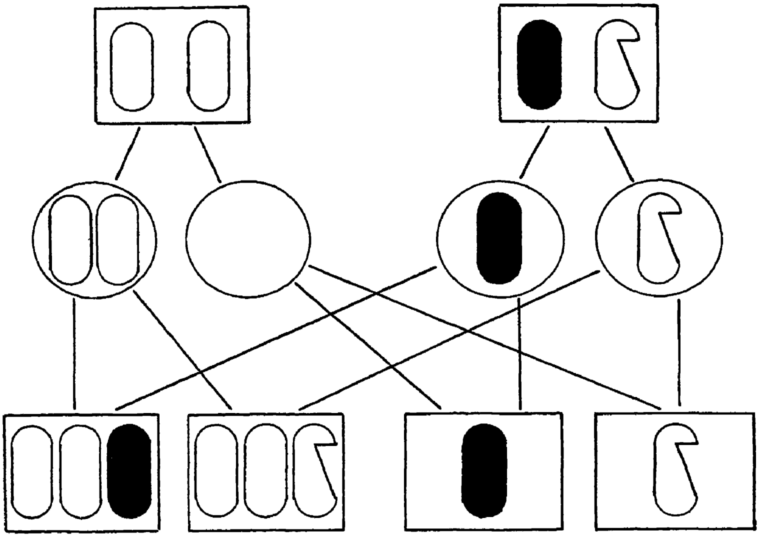

FIG 30—Showing the four types of zygotes which result from matings between non disjunctional eggs of vermilion female and normal sperms of red male Note particularly the second and third zygotes which produce the exceptional individuals vermilion female and red male

An O egg with a (VX) sperm gives a (VX) zygote which produces a red male

An O egg with a Y sperm gives a Y zygote which dies

Inasmuch as vermilion female crossed with red male normally gives only red daughters and only vermilion sons the vermilion daughters and red sons which result from the non disjunctional eggs appear as startling exceptions to the normal rule The occurrence of occasional individuals of these exceptional types led BRIDGES to suspect that non disjunction had taken place Later he effected a striking confirmation by cytological demonstration that the exceptional vermilion females possessed a Y chromosome and that the exceptional red males had no Y chromosome This work provides the final convincing demonstration that the chromosomes are the bearers of hereditary characters since abnormalities in the distribution of a certain chromosome set are accompanied by corresponding abnormalities in the distribution of those genes which were assumed to be located on that chromosome set

In the chapter on bud variation the phenomenon of chromosome elimination was discussed (p 1 1) MORGAN and BRIDGES (17) have discovered this sort of thing in connection with the sex chromosomes in the fruit fly An individual which starts its development as a normal female XX has one of the Y chromosomes eliminated from one of the daughter cells at an early embryonic division Tissues arising from this daughter cell have only one X chromosome and show the characteristics of the male sex while the rest of the tissues are female Individuals of this part female—part male type are known as *gynandromorphs*

PHYSIOLOGICAL THEORIES —In 1906 HERTWEG (14) performed some sex determination experiments with frogs The eggs are laid free in the water before fertilization so that they furnish unusually good material for such experiments Normally the eggs are fertilized very soon after they are laid with the result that the progeny consists of approximately 50 per cent males and 50 per cent females HERTWEG took some of these eggs and allowed them to overripen before fertilization took place that is he put aside some eggs as soon as they were laid and allowed them to remain unfertilized for an unusually long period While these eggs were standing in the water he found that they absorbed an unusual amount of water and the obvious conclusion was that overripe eggs show high water content He then allowed these overripe eggs to be fertilized and the resulting progeny were 100 per cent males His conclusion was that sex was not determined by the chromosome equipment but by the physiological conditions of the egg high water content resulting in males

This theory was confirmed in a striking way in 1912 by Miss King (15) who performed the converse of Hertweg s experiments using toads eggs Taking some newly laid eggs she withdrew water from them then allowed them to be fertilized and the resulting progeny were 90 per cent females The obvious conclusion is that eggs with low water content produce females

Finally there is the remarkable work of Riddle (18) with pigeons Hertweg and Miss King had found that sex is determined by the physiological factor of water content Riddle has investigated the matter a little more fully and from his analysis of the physiological conditions of male and female he gives the following contrasts

M l	F l
High percentage of water	Low percentage of water
Low percentage of fat	High percentage of fat
Low percentage of phosphorus	High percentage of phosphorus
High rate of metabolism	Low rate of metabolism

It appears from this that high water low fat and low phosphorus are male attributes or conditions while the female attributes are the reverse The main feature of difference however to which the other contrasting conditions are subordinate is that the male shows high metabolism and the female low metabolism The idea is that any physiological conditions that affect water content fat content or phosphorus content or through these (or otherwise) the metabolic rate in the egg will affect the sex of the resulting progeny

Following these ideas RIDDLE was able to control the sex ratio by various means Furthermore he makes the somewhat startling statement that sex is a quantitative phenomenon that is the difference between male and female is a difference in degree only A diagram (fig 31) will illustrate the situation It represents a graduated scale based on the physiological condition of

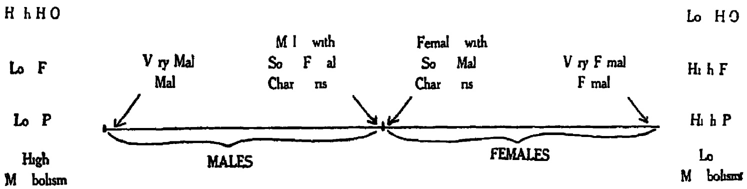

FIG 31 —Illustrating RIDDLE's idea of se Sexes differ onl quantitatively and it is possible to find various degrees of maleness and femaleness at different points alon the scale

the egg The egg may be at any point on the scale and the sex of the individual produced by the egg will depend upon its position on the scale An egg in any position to the left of the middle results in a male and to the right in a female It should be noted that if the egg is near one of the extremes the progeny will be either a very masculine male or a very feminine female while if the egg lies near the middle point on one side or the other the progeny will be a male with some female characteristics or a female with some male characteristics in other words a feminine male or a masculine female In fact RIDDLE was actually able to bring this about obtaining at will males with all degrees of maleness etc

This mechanism of sex determination suggests the following conclusions which contrast sharply with the corresponding conclusions that were drawn from the sex chromosome mechanism

a) The sex ratio has no fixed value but may be modified artificially through manipulation of the effective physiological conditions

b) Sex is a quantitative matter strictly male and strictly female being merely the two extremes between which there may occur various grades of intersexes or sex intergrades

Having as a background these two contrasting theories on sex determination in animals we may consider briefly some of the situations that have been uncovered in the plant kingdom A few meager bits of evidence suggest a sex chromosome mechanism in plants

STRASBURGER (22) has described some experiments with the liverwort *Sphaerocarpus* which is peculiarly favorable material for such work It is dioecious like many liverworts but a remarkable feature is that the spores hang together in the tetrad Ordinarily when spores mature the tetrads are no longer distinguishable Sowing such free spores one may get the 50–50 ratio of male and female gametophytes but this is no sure indication that the sexes are evenly divided in every tetrad it may have been only an equal division in the capsule as a whole *Sphaerocarpus* however provided an opportunity to test this matter for one could isolate mature individual tetrads the four spores hanging together When such tetrads were sown in separate pots four gametophytes were obtained in most cases and practically always two of the gametophytes were male and the other two female This behavior certainly suggests an even separation of the sexes at the reduction division such as would be brought about by the sex chromosome mechanism

More recently ALLEN (1) after repeating and confirming the foregoing experiment made a systematic cytological search for the X chromosome in *Sphaerocarpus* He now reports that one large chromosome (X) exceeding in length and thickness the other chromosomes characterizes the cells of the female gametophyte while the cells of the male gametophyte are characterized by one very small chromosome (Y) His investigation shows that in spore formation two of the spores of the tetrad receive the large chromosome while the other two receive the small chromosome

This rather clearly establishes a sex chromosome mechanism but the situation is distinctly different from that in animals The sex chromosome mechanism in animals provides for a differentiation of sexual individuals in the diploid generation the female being XX and the male XY The sexual individuals in *Sphaerocarpus* however are of the haploid gametophyte generation the female gametophyte regularly being X the male Y and the sexless diploid sporophyte generation being regularly XY In the animal mechanism sex is really established only at the time of fertilization while in *Sphaerocarpus* it is established immediately at the reduction division

MARCHAL (16) has done an interesting bit of work which further provides indirect evidence on a sex chromosome mechanism for sex determination in the gametophyte generation *Funaria* is a dioecious moss and hence it may be assumed that the sexes are separated at the reduction division in the formation of spores Each spore carries the potentialities for one sex only but of course the sporophyte as a whole before the reduction division must carry the potentialities for both sexes MARCHAL by a peculiar technique of his own clipped a fragment from a young sporophyte and induced it to reproduce aposporously that is the sporophyte fragment produced a gametophyte directly The fragment must have contained the potentialities for both sexes since it consisted of tissue in which the reduction division had not yet occurred Presumably the resulting gametophyte should be bisexual producing both antheridia and archegonia and this was the result actually obtained It is quite in accord with the sex chromosome theory and a striking confirmation of it

If one is to find in plants a sex chromosome mechanism comparable to that of animals he must look to the cases where the diploid sporophyte generation shows a sexual differentiation of individuals such as in dioecious angiosperms SANTOS (19) working with *Elodea* has shown that in the tissues of the male plant there regularly occurs (in addition to certain even pairs of autosomes) one uneven pair of chromosomes of which the larger member may be designated as *X* and the smaller member as *Y* He has further demonstrated that the reduction division serves to separate the members of this pair so that half of the pollen grains contain an *X* chromosome and the other half contain a *Y* chromosome Preliminary examination suggests that the tissues of the female plant are regularly of the *XX* constitution but this part of the work has not yet been completed There seems little doubt however that here is a sex chromosome mechanism exactly equivalent to those found in the animal kingdom Two types of pollen grains *X* and *Y* produced in equal numbers and mating with (pre sumably) one type of egg *X* result in 50 per cent female individuals *XX* and 50 per cent male individuals *XY*

Indirect evidence of a sex chromosome mechanism in angiosperms is provided by some of the experiments of CORRENS and SHULL CORRENS (12) crossed the dioecious *Bryonia dioica* with the hermaphroditic *B alba* while SHULL (21) crossed *Lychnis dioica* with hermaphroditic mutants from the same The sexual behavior of the progenies in the two cases was not identical but both suggested a sex chromosome mechanism with the male heterozygous for sex (The theoretical explanations however are so complex and dubious that they cannot conveniently be discussed here)

More recently CORRENS (11) working with *Melandrium* (*Lychnis*) has uncovered an interesting phenomenon which might be interpreted as indicating a sex chromosome mechanism and a type of sex linked inheritance It is assumed that pollen grains of the two types are produced in equal numbers but that the female determining grains (*X*) contain a gene which hastens pollen tube growth while the male determining grains (*Y*) lack this gene When a deficient amount of pollen is applied to the stigmas the resulting sex ratio is 44 per cent males 56 per cent females When a large excess of pollen is applied so that competition between male determining and female determining pollen tubes is more severe the resulting sex ratio is 3 per cent males 68 per cent females A moderate excess of pollen results in 40 per cent males 60 per cent females

At the present date there is probably more evidence to support physiological theories of sex determination in plants It should be borne in mind that the majority of plants are bisexual individuals and that such cases are hardly comparable with unisexual animals Very often in bisexual plants the male and female gametes are produced at slightly different stages in the life cycle and the interpretation of such phenomena is usually sought in terms of physiological conditions A young fern prothallium frequently produces antheridia only while a mature prothallium produces archegonia only In attempting explanation it is usually stated that more nutrition is required for the production of archegonia and eggs than for the production of antheridia and sperms During the flowering season monoecious angiosperms (e g *Begonia*) will sometimes produce the male flowers distinctly earlier than the female flowers or the reverse In connection with such cases botanists usually feel that the potentialities for both sexes are at all times present in all the tissues of the individual and that it remains for some unknown complex of physiological conditions to call out one or the other sex in any given region of the plant Surely no sex chromosome mechanism can be at play to account for sex differentiation here Only by assuming a reduction division some time during somatogenesis or a regular and periodic chromosome elimination could such cases be brought in line with the sex chromosome mechanism of sex determination It is much more reasonable (for the present at least) to regard bisexual plants as outside the scope of the sex chromosome mechanism

In unisexual plants one is confronted by a different situation and sometimes as discussed above a sex chromosome mechanism seems to be determining sex Even here however it would doubtless be possible to cite more evidence favoring the physiological theories Angiosperms that are normally dioecious have frequently produced bisexual plants that might well be regarded as intersexes Considerable work has been done to indicate that various environmental conditions may either modify the sex ratio or result in the production of inter sexes A favorite subject for such experiments is *Cannabis* and many investigators have succeeded in a certain amount of artificial manipulation of sex in this form SCHAFFNER (20) has gone so far as completely to reverse the sex of given individuals by modifying the cultural conditions He voices the belief of many other botanists when he draws the following conclusions

Sexuality is a state or condition not Mendelian in nature but related to functional activity of the plant and profoundly influenced by environment Maleness and femaleness in hemp are probably controlled by the metabolic level of the cells and sex reversal takes place when the metabolic level is decidedly changed or disturbed Any tissue in its growth may be in a neutral state of varying degrees of intensity and during its continued growth can pass from one state to the other without any reference to chromosome segregation or combination which are the ordinary causes of Mendelian phenomena

The situation might be clarified somewhat by the following generalization Not only are there relatively fewer plants than animals in the unisexual condition but even in those plants that are unisexual this condition is not so completely established as in animals The sex chromosome mechanism seems to operate only in organisms where the purely unisexual condition prevails and has prevailed for some time back in their phylogenetic history Many of the dioecious angiosperms however seem rather recently to have been derived from ancestors which have the two sexes represented in the same flower (or at least on the same plant) In these the dioecious condition seems not to have been firmly estab lished a regular sex chromosome mechanism has not as yet been perfected

It is small wonder that bewildering sex conditions appear in these imperfectly dioecious angiosperms SCHAFFNER and others have pointed out how extrinsic factors may operate to determine sex in such forms It is evident though that intrinsic hereditary factors may also play their part in such cases This may be illustrated by some of the experiments of STRASBURGER (22) on *Mercurialis* (later confirmed by YAMPOLSKY 23) STRASBURGER had the idea that the pollen mother cell develops pollen grains with stronger and weaker male tendencies while the megaspore mother cell develops eggs with stronger and weaker female tendencies It is therefore the algebraic sum of the two as they meet in fertilization that determines the sex of the progeny If a pollen grain with strong male tendencies mates with an egg with weak female tendencies the resulting individual will be male and similarly for the other combination These assumptions are supported by the behavior of *Mercurialis* This form has for the most part pure male and pure female individuals but at times it throws intersexes of various grades Certain plants are prevailingly female but bear a few weak male flowers In a plant of this sort it would seem that the female tendencies are stronger than the male When such a plant is inbred using pollen from the weak male flowers on the stigmas of the strong female flowers the resulting progeny is all female which is in accordance with STRASBURGER s theory Other plants are prevailingly male but bear a few weak female flowers and inbreeding these results in all males Finally there are some plants which are evenly monoecious half their flowers being strong males and the other half strong females Inbreeding such plants yields a progeny which is 50 per cent male and 50 per cent female It is obvious that from such results STRASBURGER would be convinced of his theory of male and female tendencies

Of considerable interest to botanists is some work that has been done on the sexual condition of *Mucor* and related genera of fungi BLAKESLEE (2 3) found three different sexual types of mycelia two of which he called plus and minus strains

Although they looked alike in every particular he concluded that they were sexually different for the following reason Neither strain by itself is capable of producing zygotes but when plus and minus strains are brought together sexual branches from the one meet sexual branches from the other and produce abundant zygotes The natural conclusion is that BLAKESLEE s plus and minus strains represent the male and female conditions although the sex cannot be distinguished by direct examination The third type of mycelium he called the neutral strain for it is incapable of producing zygotes in any combination

The answer to the question as to where sex is determined in these forms is as follows When a zygote germinates one or more sporangia are produced very early and individuals are multiplied by the spores from these sporangia In *Mucor* itself the segregation of sex is evidently completed before the formation of spores in this first sporangium for all of its spores will produce the same strain of mycelium The sporangium as a whole therefore is either male or female In *Phycomyces* however a different behavior appears The zygote produces a sporangium but the sporangium is not completely of one sex It produces three types of spores spores producing the plus strain spores producing the minus strain and spores producing the neutral strain The plus strain then perpetuates only plus strains through its spores which means that sex is fixed in this case The minus strain behaves in a similar manner The neutral strain however produces spores of all three types an interesting situation for it suggests Mendelian segregation

BURGEFF (8) has performed an interesting operation on this same material By means of a very careful technique he grafted parts of the plus strain on to the minus strain and secured graft hybrids with the characteristics of the neutral strain In attempting to interpret the foregoing results it should be remembered that *Mucor* and its relatives are coenocytic so that nuclei of two types can mingle freely in the mycelium

Proceeding further with this material BLAKESLEE (4) isolated numerous plus and minus strains and found that they differed in their sexual intensity as computed in terms of the number of zygotes formed under standard conditions Evidently some strains are more strongly plus (female as was later determined by indirect means) and others less strongly plus and the same was true of the minus (male) strains This strongly suggests a quantitative interpretation of sex

Recently BURGEFF (9) has discovered some startling facts in connection with sex in some of the other genera of Mucorineae *Absidia* shows the customary plus and minus strains as does also *Parasitella* This latter genus is a parasite upon other genera of the same family and in connection with this parasitic habit there appears a remarkable situation The plus strain of *Parasitella* will parasitize the minus strain of *Absidia* but not the plus strain of *Absidia* while the minus strain of *Parasitella* will parasitize the plus strain of *Absidia* but not the minus strain of *Absidia* The author concludes that the hypothetical sexual substance which distinguishes the plus and minus mycelia of *Absidia* is identical with the substance that induces parasitism and that the parasitic relationship here has arisen as the result of an unsuccessful attempt at hybridization between the two genera

The discussion to date leaves the interpretation of sex determination in a distinctly unsettled condition We find that in a great many animals and a very few plants a very definite sex chromosome mechanism operates to determine sex and that sex is a qualitative proposition only the two conditions of strictly male and strictly female being possible On the other hand it is suggested by the sexual behavior of some animals and quite a number of plants that the general physiological condition is important in determining sex and that sex is a quantitative matter intersexes or sex intergrades being possibilities that are frequently realized

There are three possible conclusions with reference to these contradictory theories (1) an acceptance of one and rejection of the other (2) the claim that both amount to the same thing that they express the same fundamental facts in different terms or by the use of different indices (3) the claim that both are true but cover different territories that one of them explains certain types of cases and the other explains other types of cases

Until very recently the third alternative seemed the most acceptable inasmuch as the two types of sex determining mechanism had never been clearly identified in the same organism The recent work of BRIDGES (6, 7) however sways opinion to the second of the foregoing alternatives for it harmonizes the two contradictory views on sex determination to a degree that would hardly have seemed possible

An unexpected distribution in inheritance of known factors which are located on the second and third chromosomes of the fruit fly was explainable on the assumption that the female parent was triploid with respect to these chromosomes Cytological examination proved that this was actually the case The same group of flies also exhibited some remarkable irregularities in their sex condition A considerable group of intersexes occurred as evidenced by the secondary sex characters and the condition of the gonads as well (This was apparently a bimodal group some of the intersexes being of a more female type and others of a more male type) Cytological examination of these individuals revealed that the second and third chromosomes were regularly present in a triploid condition that the fourth chromosome was either diploid or triploid and that two X chromosomes were regularly present (with or without a Y chromosome) The situation is interpreted as follows

It is not the simple possession of two *X* chromosomes that makes a female or of one that makes a male The preponderance of genes that are in the autosomes tends toward the production of male characters and the net effect of genes in the *X* is a tendency to the production of female characters The ratio of 2*X* 2 *sets autosomes* produces a female while 1*X* 2 *sets autosomes* produces a male An intermediate ration 2*X* 3 *sets autosomes* produces an intermediate condition the intersex

The fourth chromosome seems to have a disproportionately large share of the total male producing genes for there are indications that the triplo fourth intersexes are preponderantly of the male type while the diplo fourth intersexes are mainly female type

According to this conception 3*X* 2 sets autosomes should be superfemales and 1*X* 3 sets autosomes should be supermales BRIDGES has actually identified such types both being sterile

It is certain that this conception will exert a far reaching influence upon the existing ideas of sex detemination In the first place it gives a somewhat more exact idea as to the elements effective in determining sex Hitherto it had been thought rather vaguely that the *X* chromosome determines sex either per se or by virtue of some special factor which it contains It is interesting now to realize that a number of factors may be influencing sex in one direction or the other and perhaps that these are identical with factors which have previously been known as playing another role A different rate of metabolism has commonly been associated with the two sexes a study of the influence of specific factors on metabolic rate now becomes significant in this connection

In the second place it furnishes an exact interpretation of intersexes on a chromosome basis Hitherto intersexes have usually been interpreted in rather vague physiological terms and have been used as an argument against the sex chromosome theory (or have been harmonized with the sex chromosome theory only by the assumption of some additional extra chromosomal influence—GOLDSCHMIDT 13) BRIDGES conception now paints a quantitative picture of sex without calling upon any other effective elements than the orthodox factors of inheritance that are located on the chromosomes Intersexes are therefore accounted for by the same general mechanism as normally produces only pure males and females in the fruit fly

In the third place the theoretical possibility of artificially controlling sex is illuminated Such control should be possible to the degree that the ordinary heritable characters can successfully be duplicated artificially BRIDGES acknowledges that the environment may affect sex within certain limits Although sex is fundamentally a quantitative proposition 1X 2 sets autosomes provides such a considerable preponderance of male inducing factors and 2*X* 2 sets autosomes provides such a preponderance of female inducing factors that only these two distinct qualitative conditions are visualized under ordinary circumstances Both of the foregoing conditions are far from the point of equilibrium between the opposite types of sex influences Under such circumstances the minor influences of single factors in one direction or the other produce no appreciable effect As a matter of fact a factor mutation in the germ plasm or an unusual combination of extrinsic physiological conditions might intervene to influence a male individual toward femaleness (or vice versa) but the individual is so preponderantly male that the effect of these minor influences are not noticeable

On the other hand in those individuals (the intersexes) where the male inducing and female inducing factors are near the point of equilibrium the minor influences of single factors in one direction or the other become noticeable In such an individual an unusual combination of extrinsic physiological conditions may swing the individual more toward maleness or more toward femaleness and these deviations will be observed This idea is borne out by the actual facts since the influence of environmental conditions upon the grade of sex in BRIDGES intersexes is noticeable but the same conditions do not produce noticeable effects upon the normal males and females The intersexes representing a condition near an equilibrium between opposite factor influences are more responsive to environmental differences more fluctuating than are the normal males and females

One might then assume that in organisms where the unisexual condition has existed for some time back in phylogeny a definite sex chromosome mechanism has been established This mechanism insures (normally) the production of two types of individuals in equal numbers those which are preponderantly males and those which are preponderantly females The grade of sex does not appear to fluctuate in response to varying environmental influences since these influences are relatively insignificant in such cases In other organisms however which have more recently been evolved from bisexual ancestors a regular sex chromosome mechanism has not yet been perfected The appropriate machinery is not yet at work to produce individuals which are preponderantly male and individuals which are preponderantly female in equal numbers Instead sex is being influenced by numerous factors which are distributed sporadically rather than in organized groups as in the fruit fly The net effect of these factor influences is commonly near to the point of equilibrium so that the organism is more responsive to environmental influences on sex grade Under such conditions the sex grade and the sex ratio may be susceptible to a certain amount of artificial control through manipulation of the effective environmental influences

Finally this work of Bridges casts a new light upon the whole subject of unit characters Careful investigation of flies which are triploid with respect to one or more chromosome sets leads Bridges to draw the same general conclusions with regard to other so called unit characters that he drew with regard to the character of sex Many characters have their degree of development influenced not merely by the presence or absence of certain single genes but by the net effect of the influences of numerous genes It is true that there is commonly one gene that exerts a greater influence on the character in question than do any other genes and it is quite common that all the other genes may be constant in their presence or absence so that only the effects of the one gene are noticeable and we identify it as the determiner of the character in question In such cases the equilibrium of opposing influences is normally being affected to a perceptible degree only by the presence or absence of a single gene Abnormal situations however may arise as the result of non disjunction of certain chromosome sets This by introducing a relatively greater number of genes which have a positive influence (or negative as the case may be) may modify the degree of expression of the character in question so that it shows a grade not previously seen

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